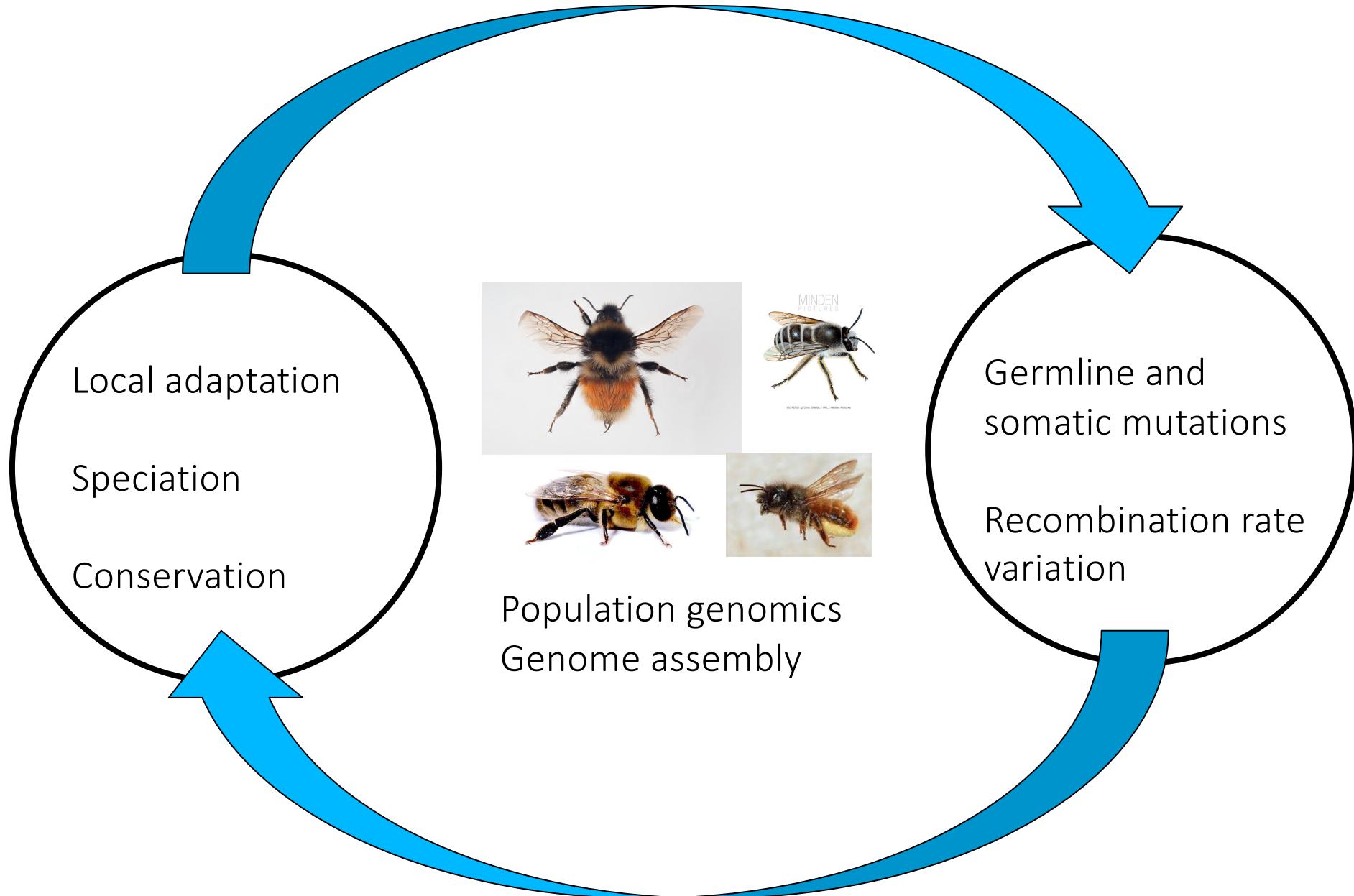


# Population genomics of arctic and montane bumblebees

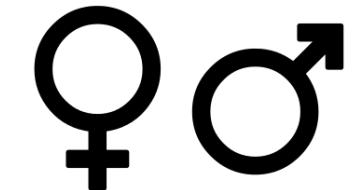
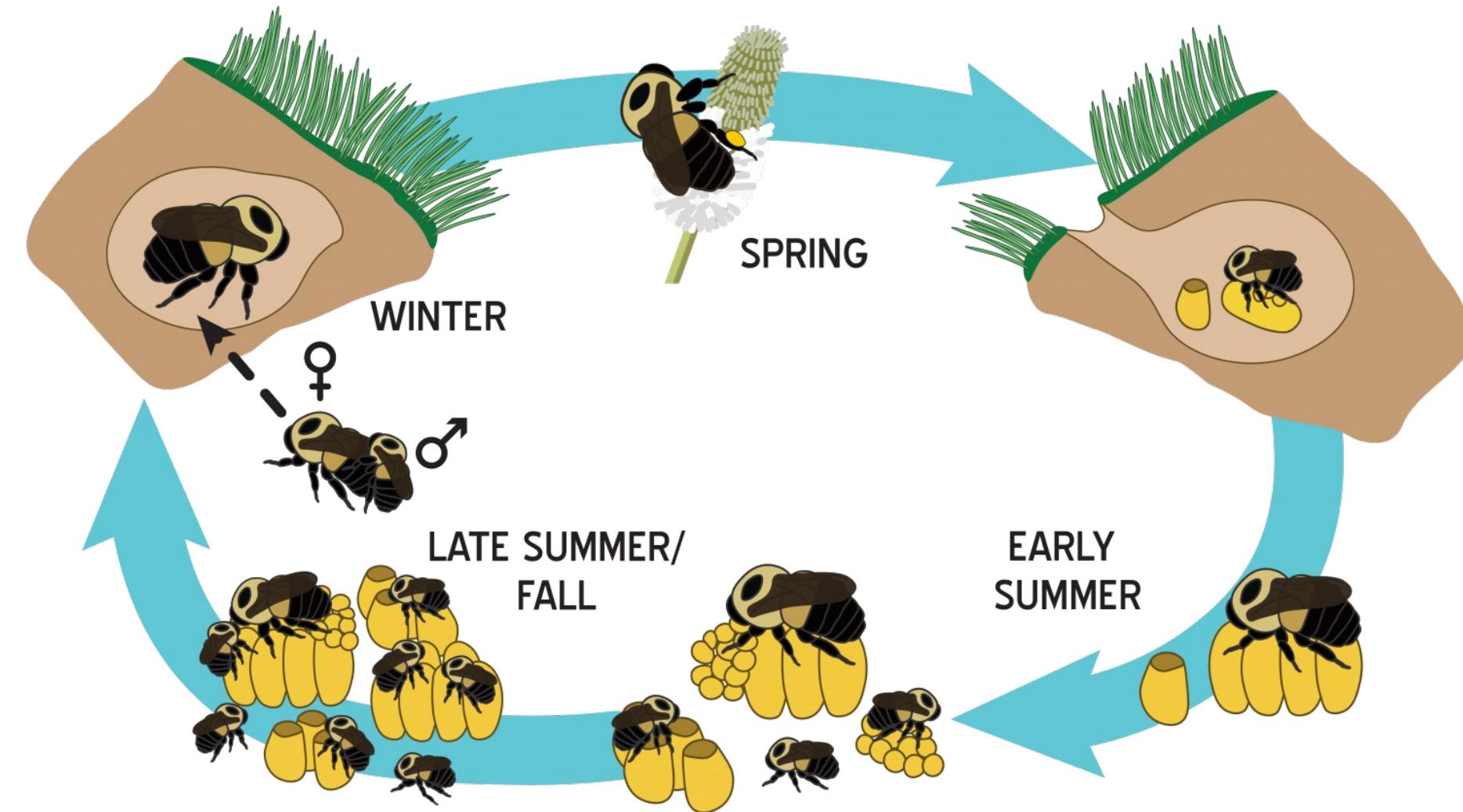


*Matthew Webster*  
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Science for Life Laboratory, Uppsala University, Uppsala, Sweden



# Bumble bees



♀	males
worker	queen
diploid	haploid
$2n$	$n$

250 species  
Cold-adapted  
Genus = *Bombus*

# Bumble bees are threatened by climate change

## CLIMATE CHANGE

### Climate change impacts on bumblebees converge across continents

Jeremy T. Kerr,<sup>1\*</sup> Alana Pindar,<sup>1</sup> Paul Galpern,<sup>2</sup> Laurence Packer,<sup>3</sup> Simon G. Potts,<sup>4</sup> Stuart M. Roberts,<sup>4</sup> Pierre Rasmont,<sup>5</sup> Oliver Schweiger,<sup>6</sup> Sheila R. Colla,<sup>7</sup> Leif L. Richardson,<sup>8</sup> David L. Wagner,<sup>9</sup> Lawrence F. Gall,<sup>10</sup> Derek S. Sikes,<sup>11</sup> Alberto Pantoja<sup>12†</sup>

For many species, geographical ranges are expanding toward the poles in response to climate change, while remaining stable along range edges nearest the equator. Using long-term observations across Europe and North America over 110 years, we tested for climate change-related range shifts in bumblebee species across the full extents of their latitudinal and thermal limits and movements along elevation gradients. We found cross-continently consistent trends in failures to track warming through time at species' northern range limits, range losses from southern range limits, and shifts to higher elevations among southern species. These effects are independent of changing land uses or pesticide applications and underscore the need to test for climate impacts at both leading and trailing latitudinal and thermal limits for species.

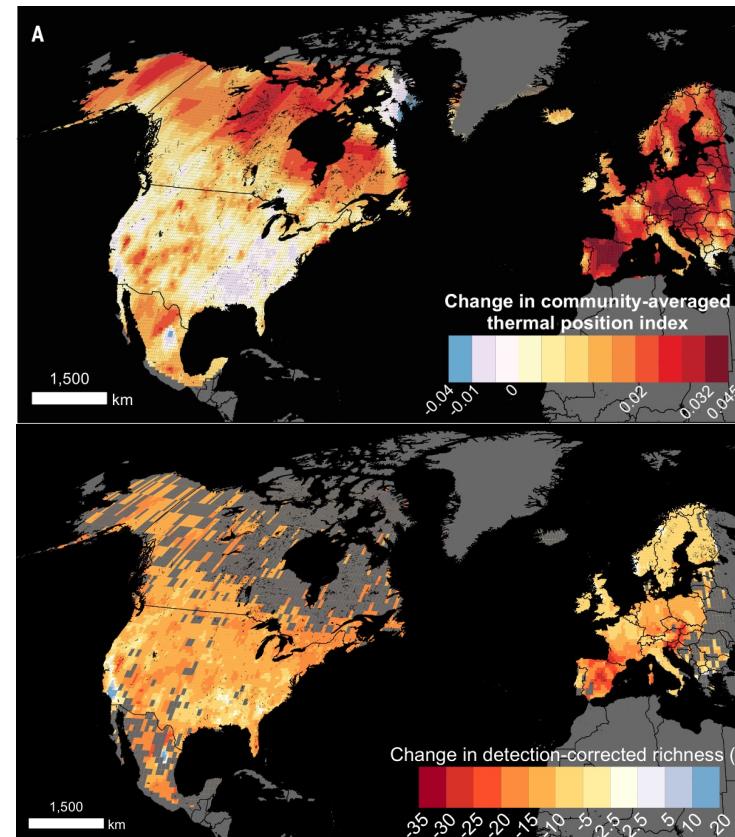
Science (2015) 349, 177–180

## POLLINATOR DECLINE

### Climate change contributes to widespread declines among bumble bees across continents

Peter Soroye<sup>1\*</sup>, Tim Newbold<sup>2</sup>, Jeremy Kerr<sup>1</sup>

Climate change could increase species' extinction risk as temperatures and precipitation begin to exceed species' historically observed tolerances. Using long-term data for 66 bumble bee species across North America and Europe, we tested whether this mechanism altered likelihoods of bumble bee species' extinction or colonization. Increasing frequency of hotter temperatures predicts species' local extinction risk, chances of colonizing a new area, and changing species richness. Effects are independent of changing land uses. The method developed in this study permits spatially explicit predictions of climate change-related population extinction-colonization dynamics within species that explains observed patterns of geographical range loss and expansion across continents. Increasing frequencies of temperatures that exceed historically observed tolerances help explain widespread bumble bee species decline. This mechanism may also contribute to biodiversity loss more generally.



- 1) Southern limits are moving north, but northern limits are not expanding
- 2) Occurrence of extreme temperatures correlated with species decline

# Arctic bumblebees



*Bombus sylvicola*



*B. lapponicus*



*B. monticola*



*B. melanopygus*



*B. bifarius*

# Initial Goals



- Genome assemblies of *B. sylvicola* and *B. balteatus*
  - Enable genomic studies of alpine/arctic bumble bee species
- Identify population substructure, connectivity and gene flow
- Genetic basis of speciation

# Sample collection in Colorado, 2017



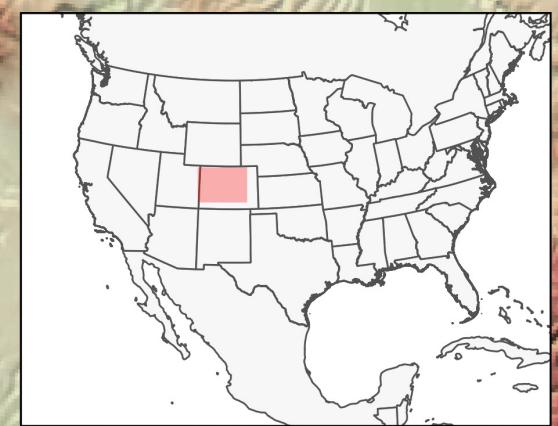
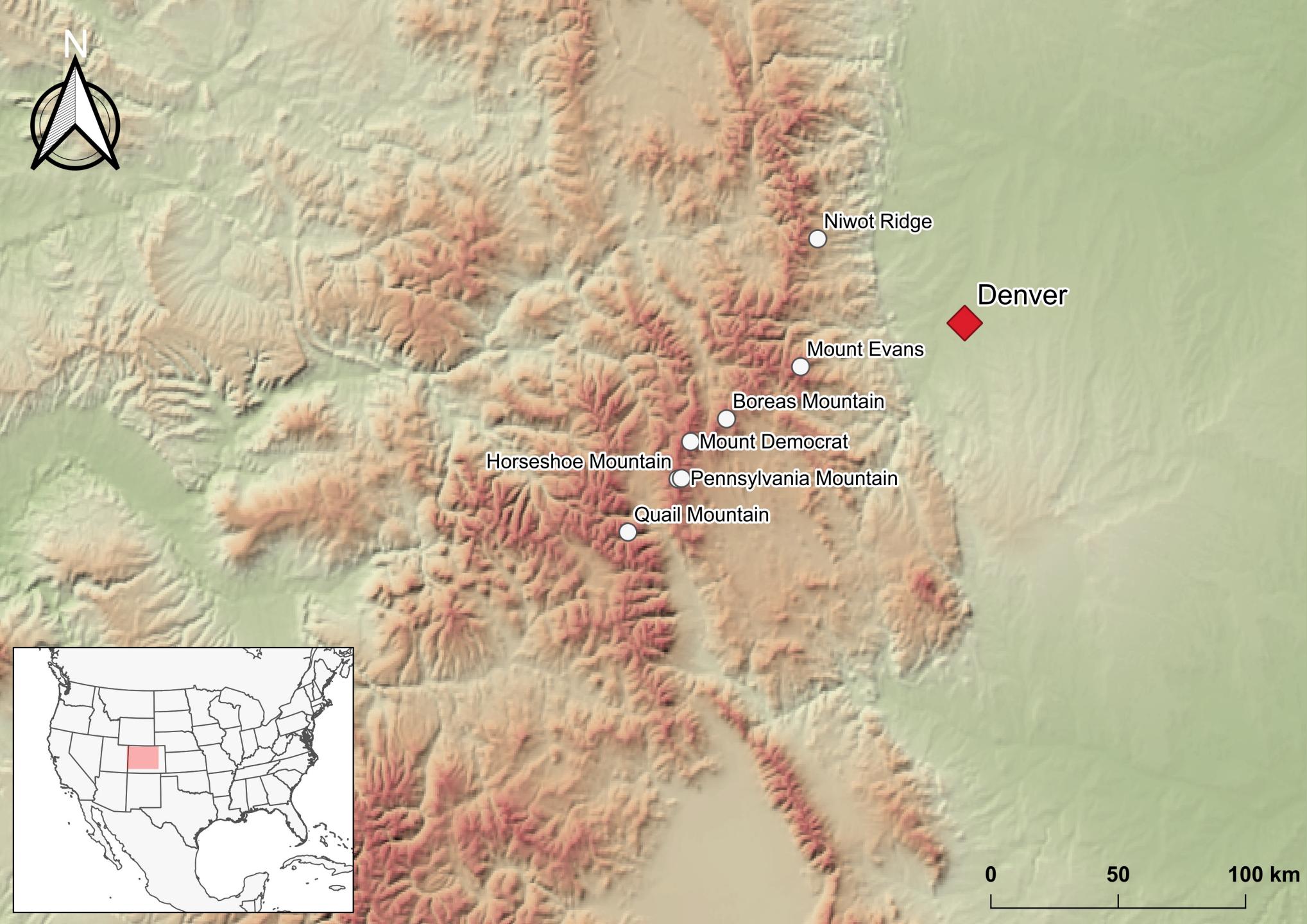
Collected ~650 samples from both species from Rocky Mountains



*B. balteatus*



*B. sylvicola*





Niwot Ridge 3700m

# Genome assemblies

(Ola Wallerman, Ignas Bunikis, Marcin Kierczak)

Assembling the genomes of *Bombus sylvicola* & *Bombus balteatus* (250 Mbp genomes)

Genome sequencing of haploid males

Oxford Nanopore – 2/3 flow cells each:

*B. sylvicola*: 17 Gbp (70x) read N50 = 6 kb.  
*B. balteatus*: 12 Gbp (47x) read N50 = 14 kb

10x Chromium – One lane of HiSeqX:

*B. sylvicola*: 67 Gbp (267x)  
*B. balteatus*: 70 Gbp (282x)

RNAseq – One lane of HiSeq 2500:

*B. sylvicola*: 44 Gbp  
*B. balteatus*: 42 Gbp



*B. balteatus*

Bioinformatics

Nanopore assembly: wtdbg2 + Racon + Medaka

10x error correction: LongRanger + Tigmint + Pilon

10x scaffolding: ARCS + LINKS

Annotation pipeline: StringTie + MAKER



*B. sylvicola*

Scaffolds placed onto *B. terrestris* genetic map to make pseudochromosomes (Satsuma)

Identification of centromeric repeats (centromere\_seeker)

## Assemblies

*B. sylvicola*: N50 = 3.1 Mbp

BUSCO = 98.6%

*B. balteatus*: N50 = 8.6 Mbp

BUSCO = 99.0%

# Comparison of assembly quality

Species	<i>B. balteatus</i>	<i>B. sylvicola</i>	<i>B. terrestris</i>	<i>B. impatiens</i>
Assembly	BBAL_1.0	BSYL_1.0	Bter_1.0	BIMP_2.2
Size (Mbp) <sup>†</sup>	250.07	252.08	248.65 (236.38)	246.86 (241.98)
Scaffolds (n)	-	-	5,678	5,460
Contigs (n)	336	592	10,672	16,060
Contig N50 (Mbp)	8.60	3.02	0.08	0.06
Contig L50 (n)	12	28	890	54
GC (%)	37.64	38.23	37.51	37.76
Repeat content (%)	17.1	17.9	14.8	17.9
Complete hymenoptera BUSCO genes (%)*	99.0	98.2	96.9	98.3

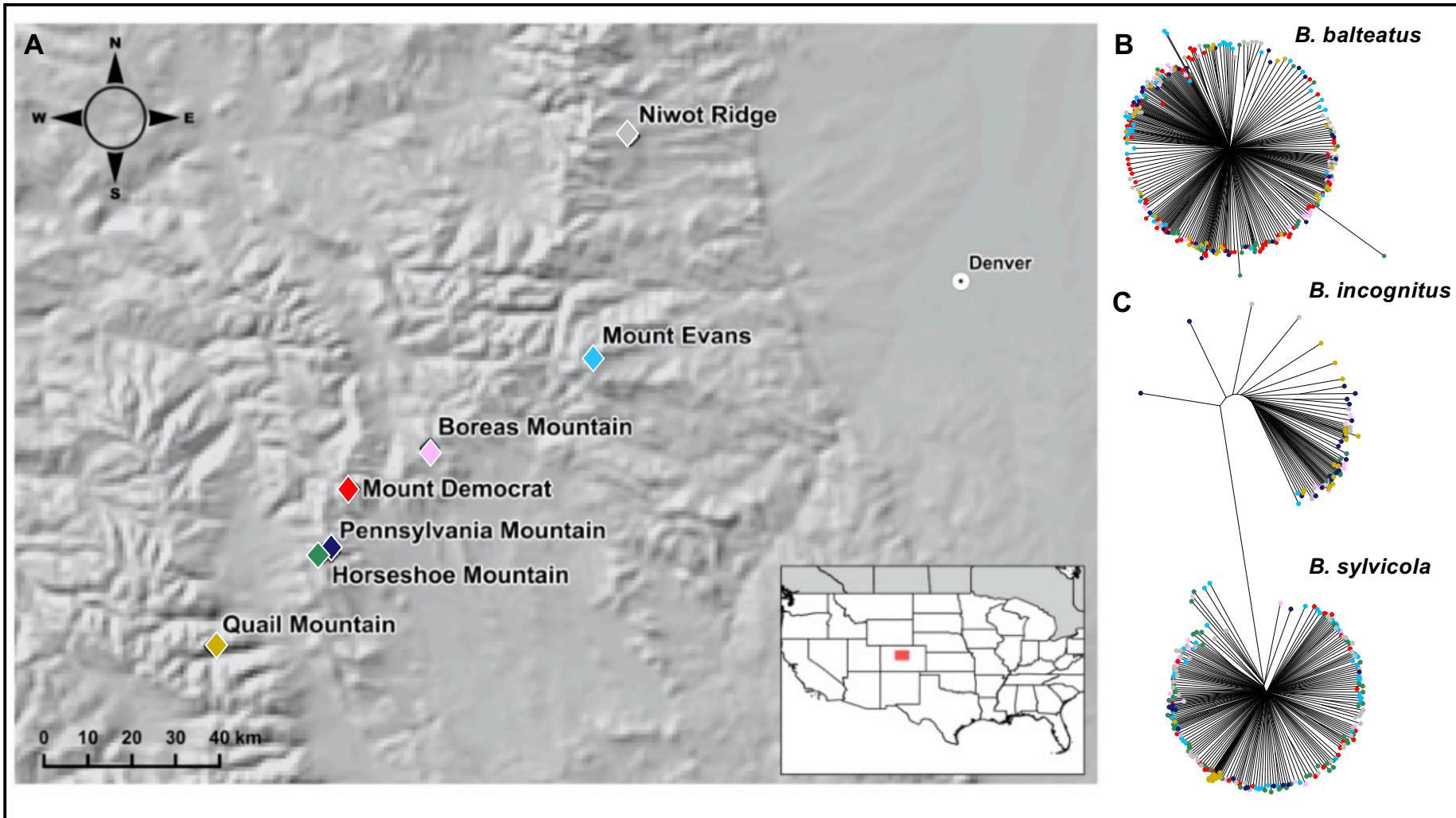
\*BUSCO analysis using the OrthoDB v. 10, Hymenoptera dataset.

<sup>†</sup> Numbers in brackets represent total ungapped length

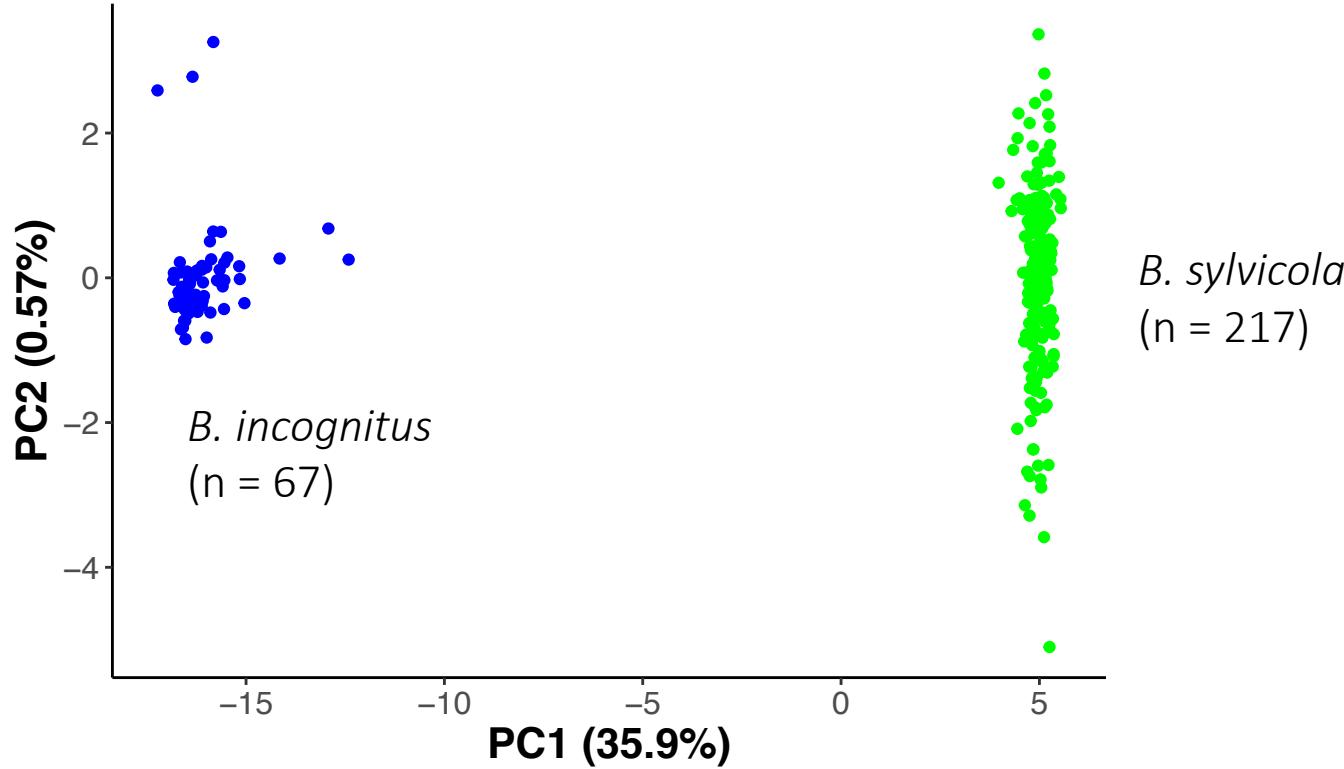
# 650 whole genome sequences of *B. sylvicola* and *B. balteatus*

Nextera Flex + HiSeqX → mean coverage ~15x

Not 2, but 3 species...



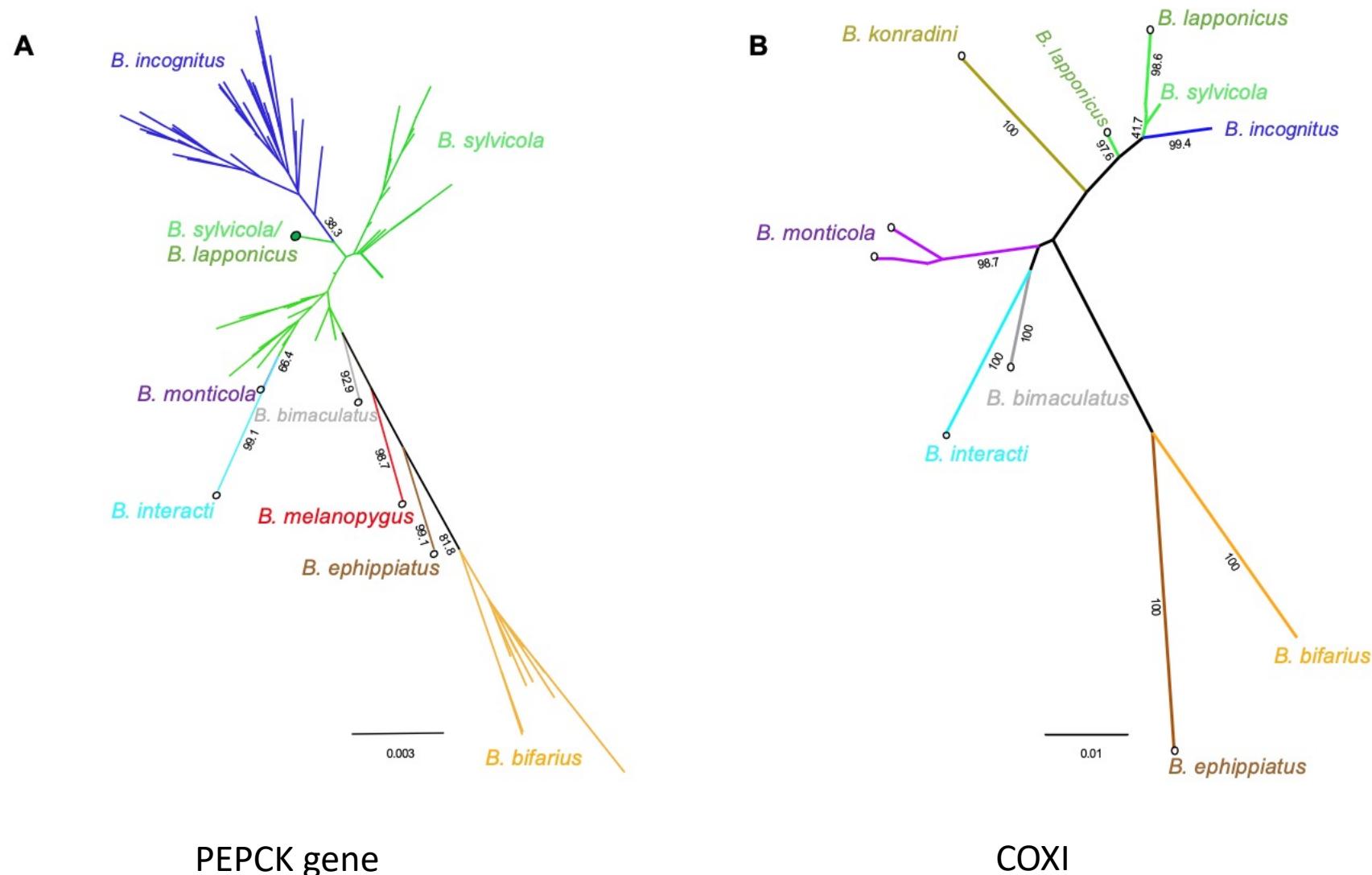
# Clustering of sequences indicates presence of new cryptic species, *Bombus incognitus*\*



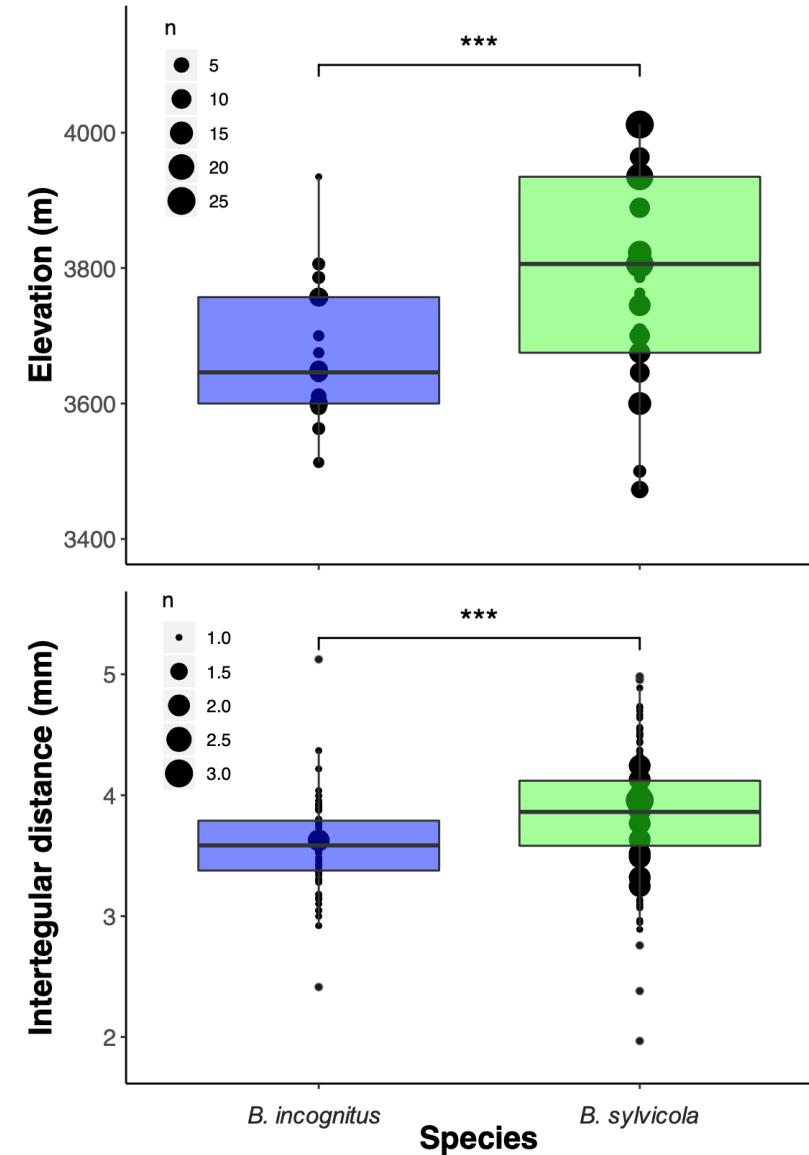
\*not official name...

- Both species identified in all localities
- No morphologically distinguishing characters identified
- No intermediates observed
- *Bombus incognitus* does not cluster with any known species by morphology or genetics

# *Bombus incognitus* is distinct from other known species



# *Bombus incognitus* tends to be smaller and found at lower elevation

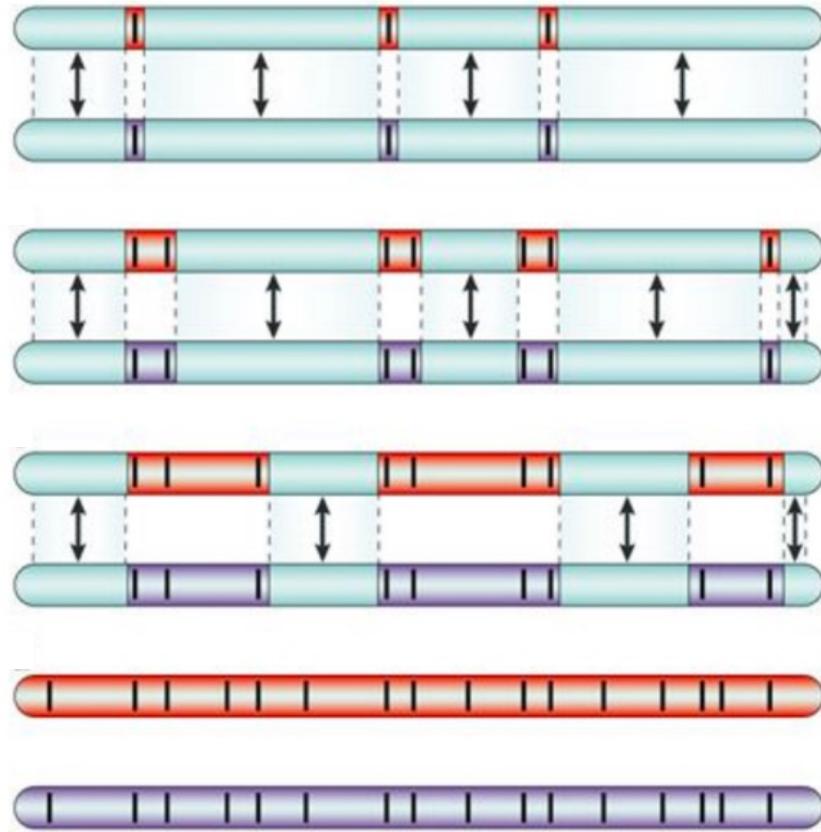


# Speciation with gene flow

early divergence



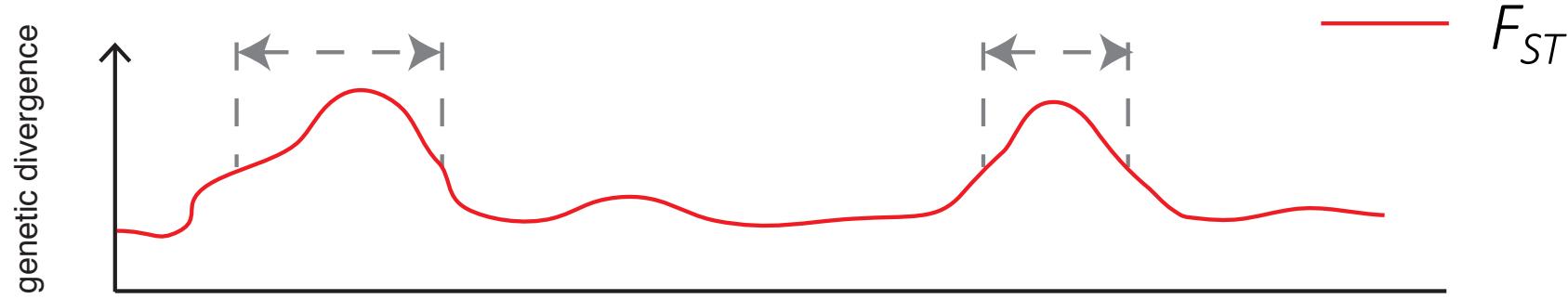
late divergence



"Islands of speciation"

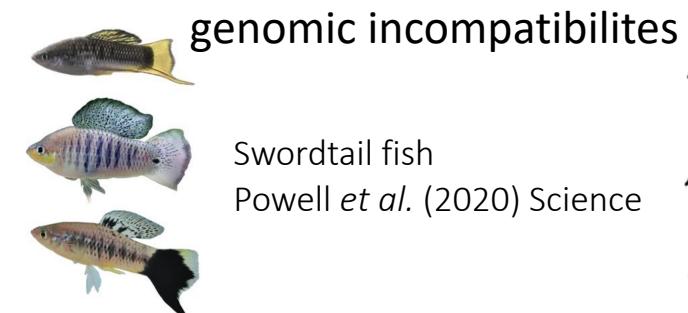
- 1) ecological specialization
- 2) genomic incompatibilities (DMIs)

# Genomic landscape of divergence shaped by multiple factors



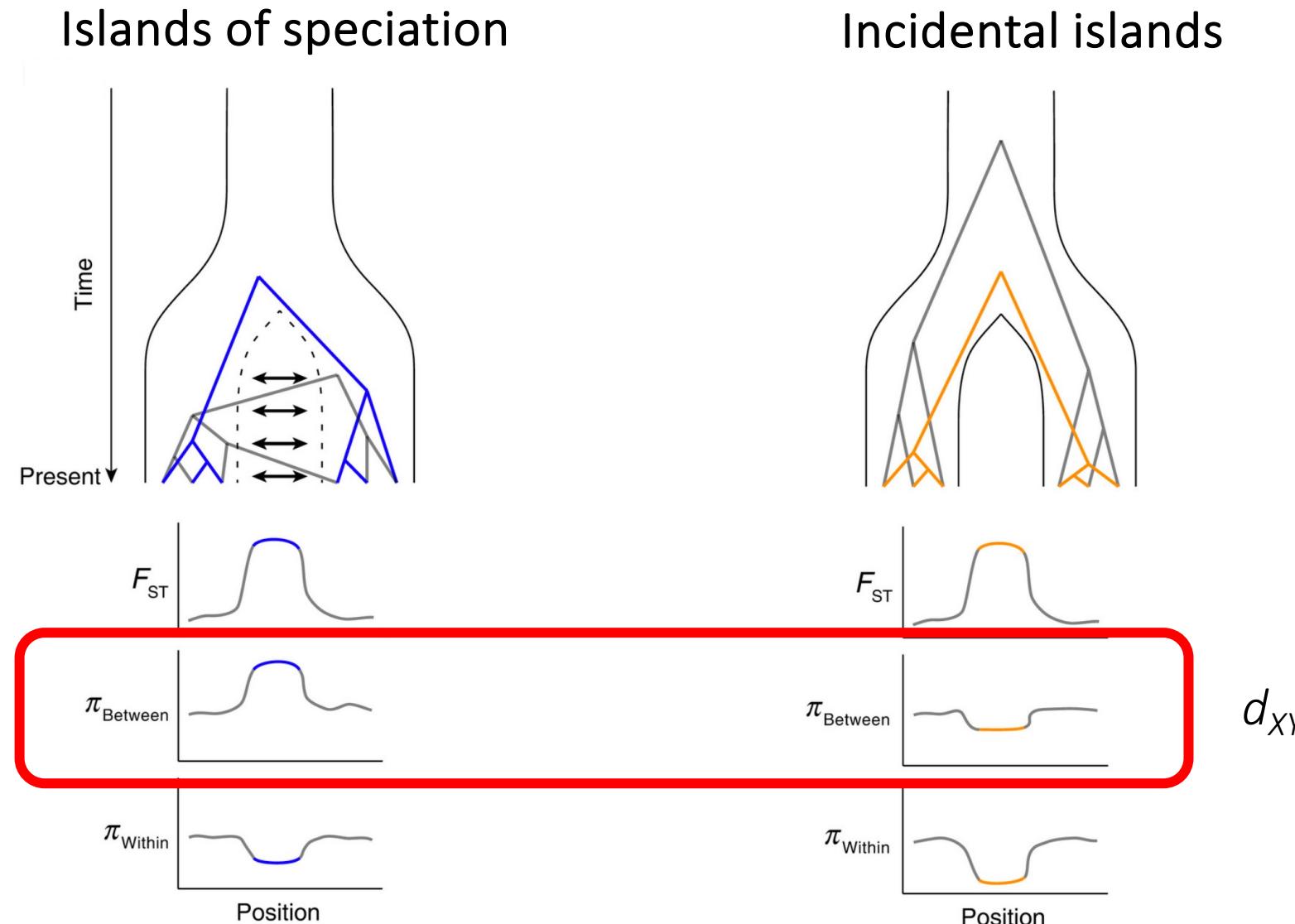
“Islands of speciation”  
resistant to gene flow

“Incidental islands”  
regions of low recombination,  
interaction with linked selection

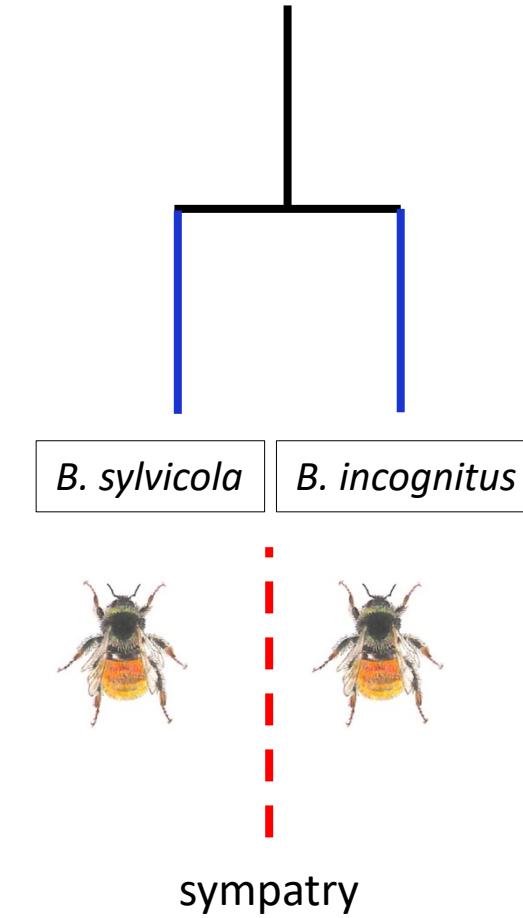
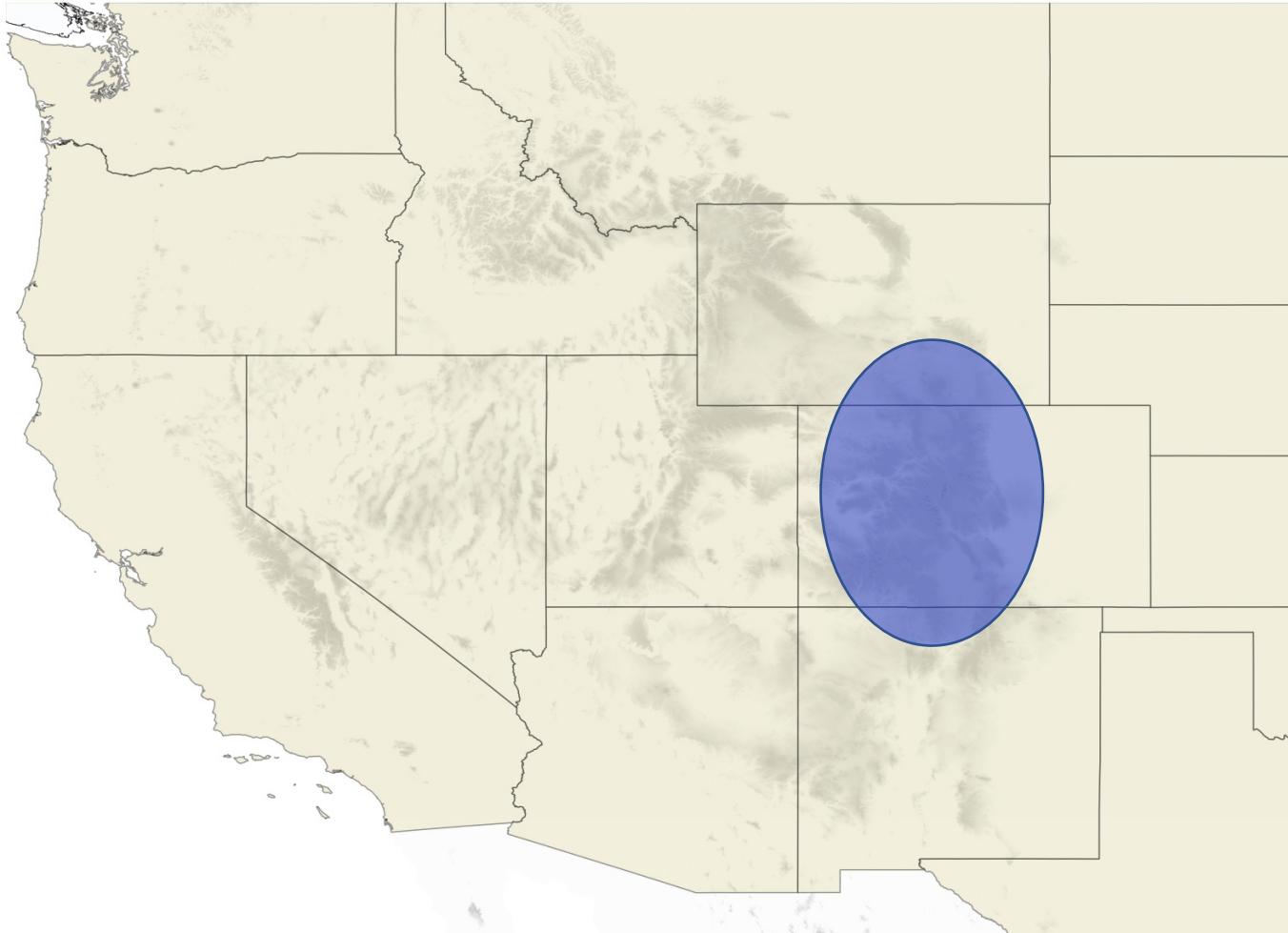


*Burri et al. (2015) Genome Res.*  
*Feulner et al. (2015) PLoS Genet.*  
*Vijay et al. (2016) Nat. Commun.*  
*Cruickshank & Hahn (2014) Mol Ecol*

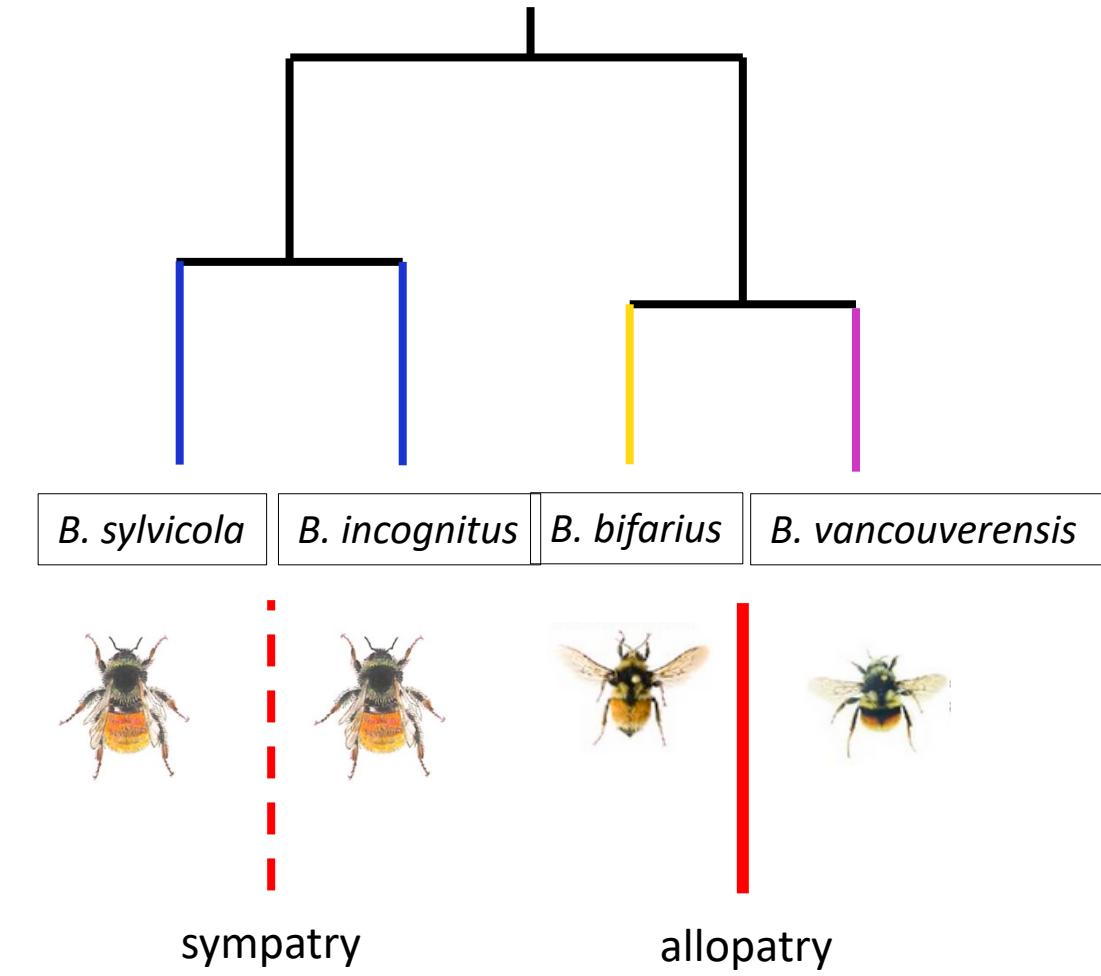
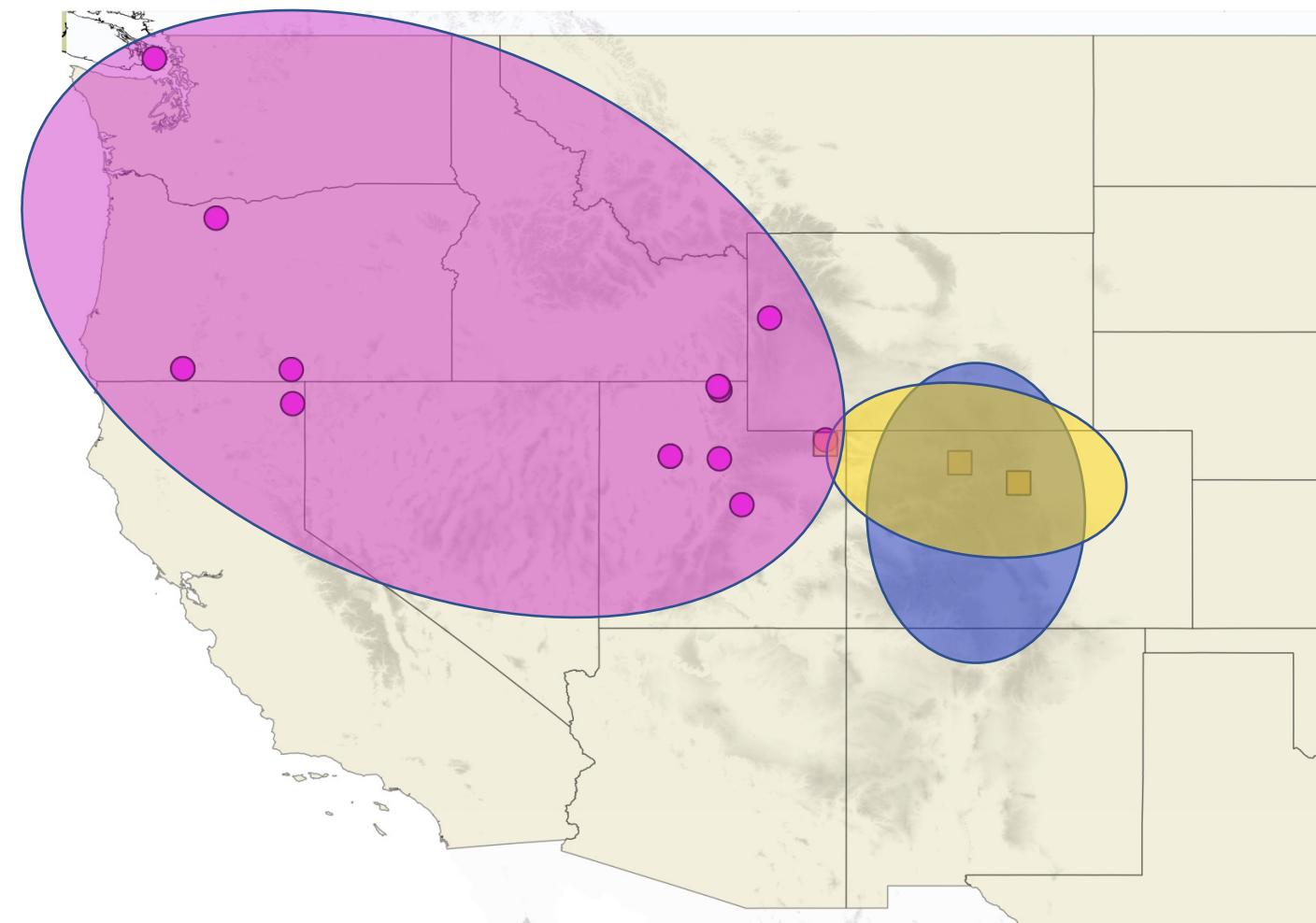
# Absolute divergence ( $d_{XY}$ ) identifies differential gene flow



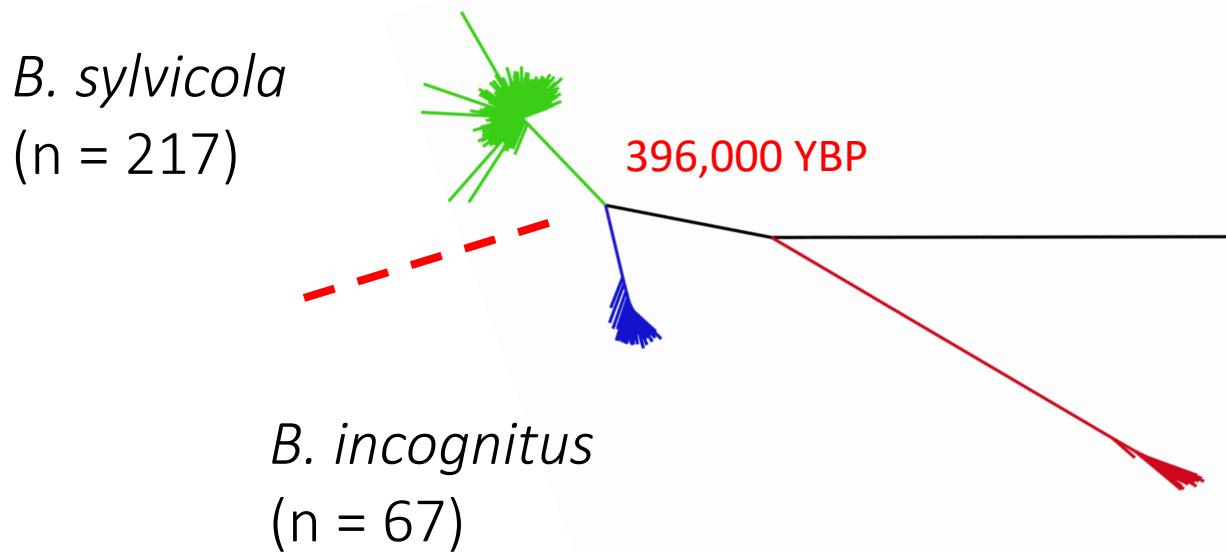
# Comparison of genome divergence in sympatry and allopatry



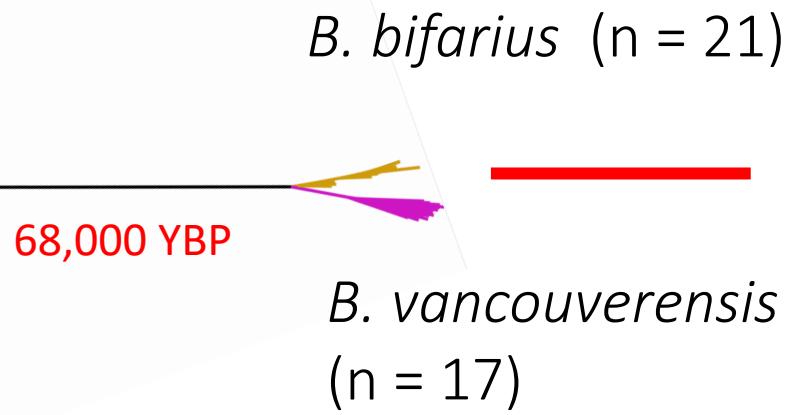
# Comparison of genome divergence in sympatry and allopatry



# Sympatry



# Allopatry



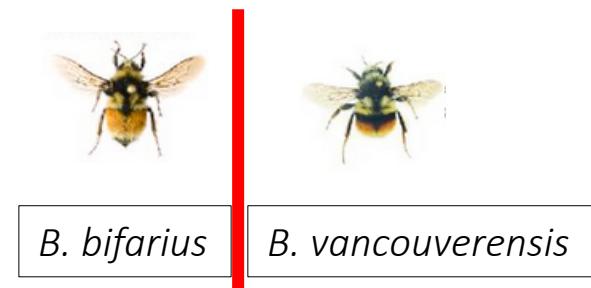
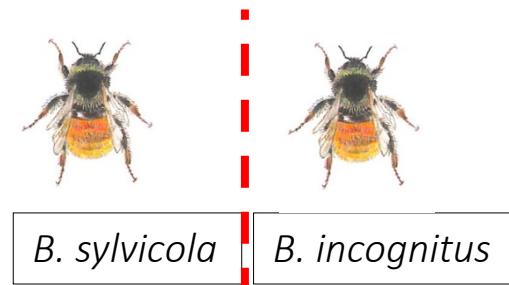
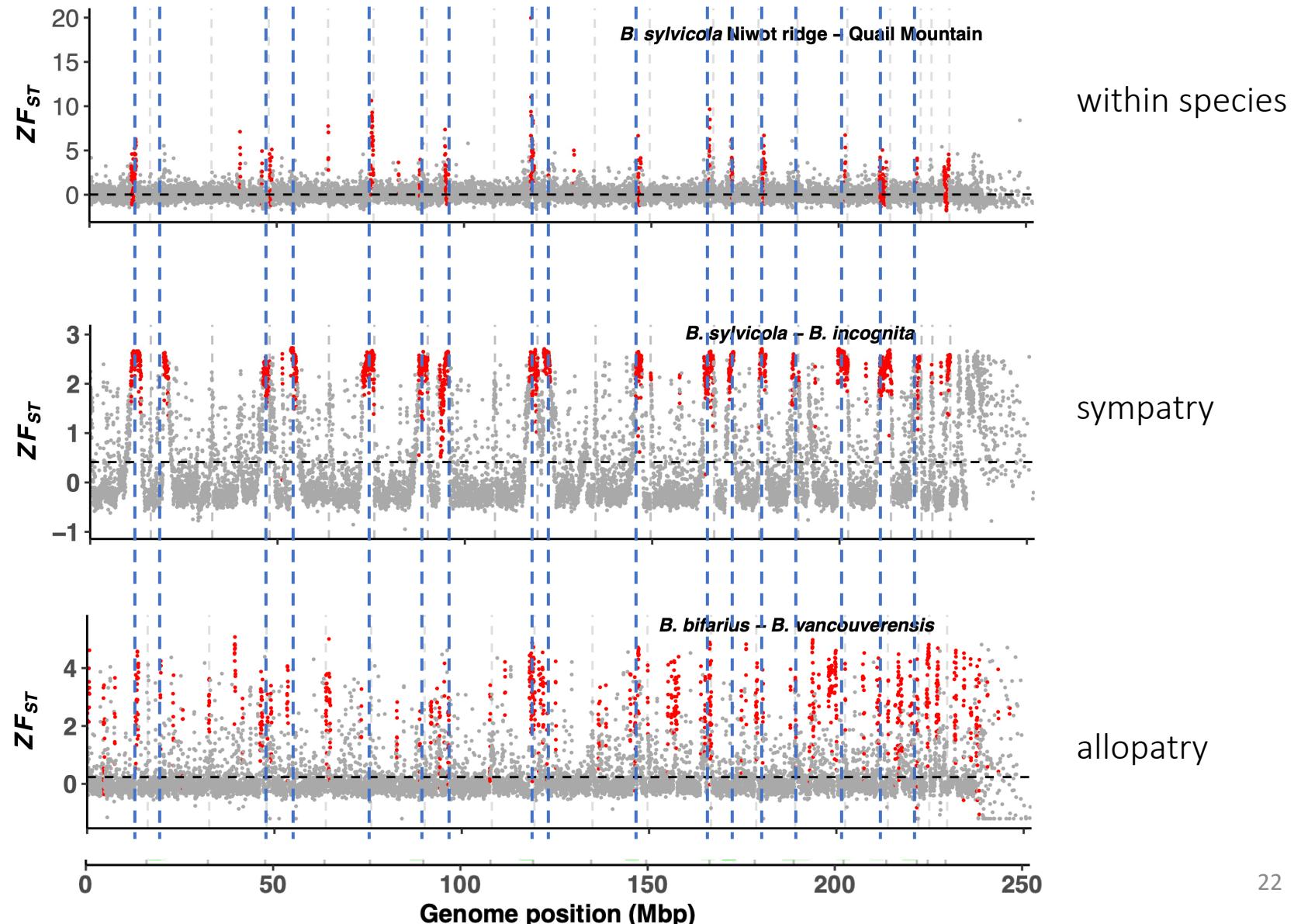
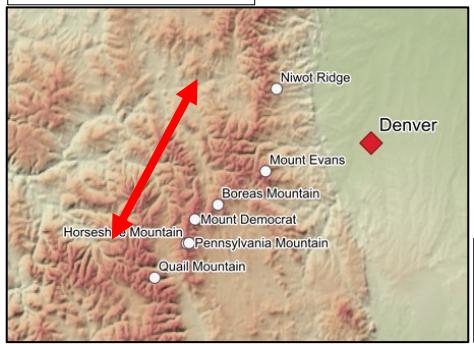
## Species

- *B. bifarius*
- *B. incognita*
- *B. melanopygus*
- *B. sylvicola*
- *B. vancouverensis*

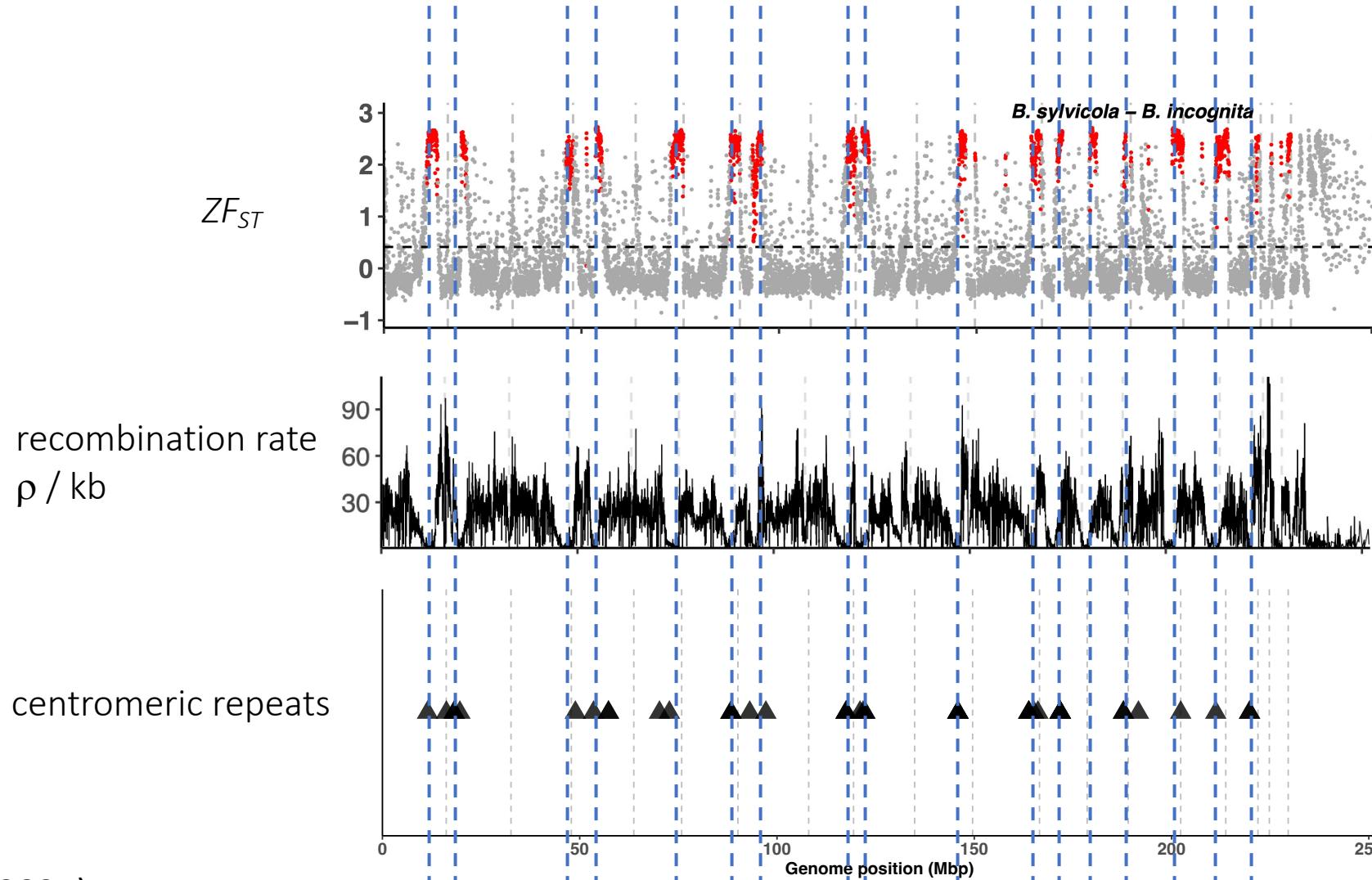
Additional data from  
Ghisbain et al. (2020) Syst. Entom.<sup>21</sup>

# Islands of divergence recur in the same genomic locations

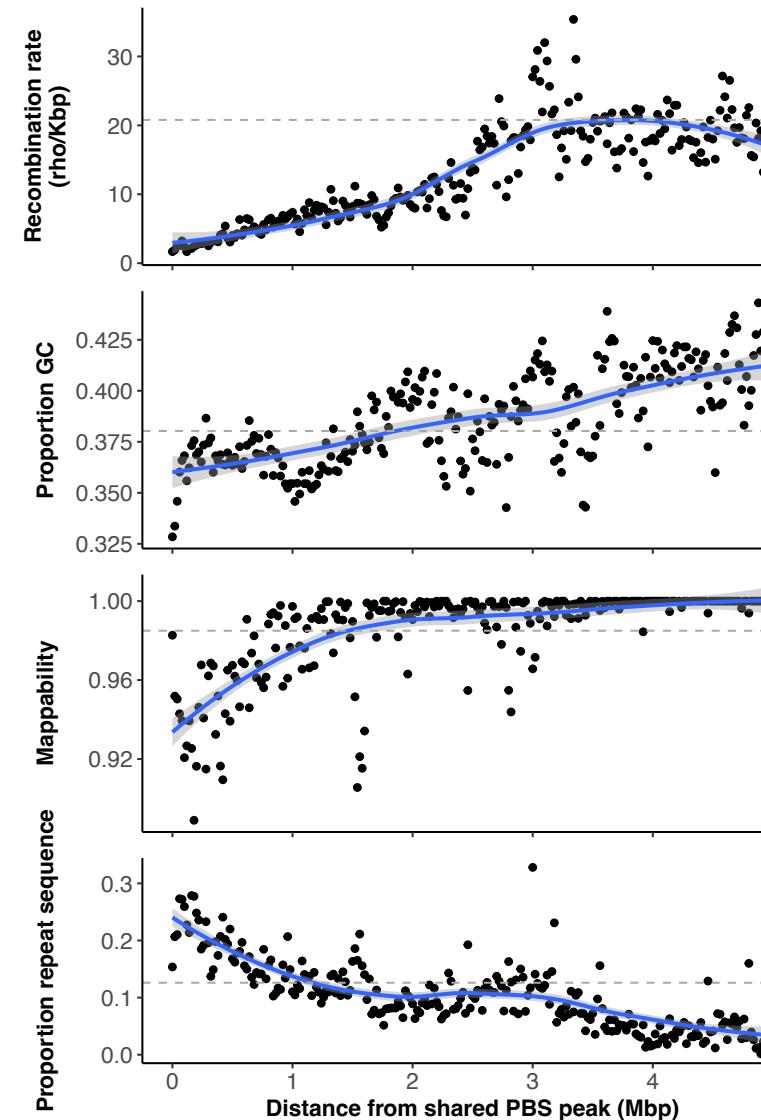
*B. sylvicola*



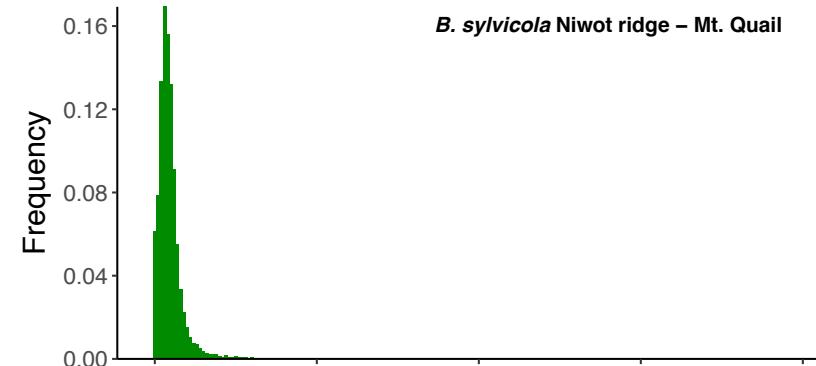
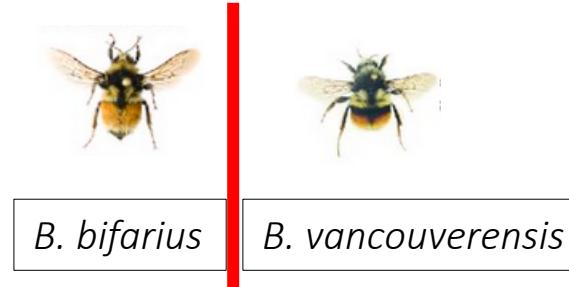
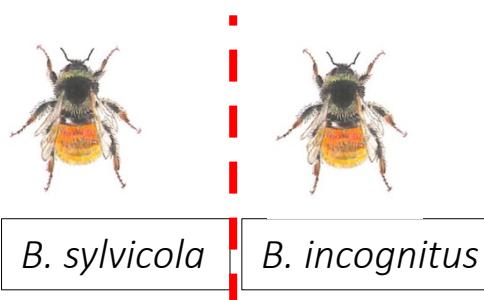
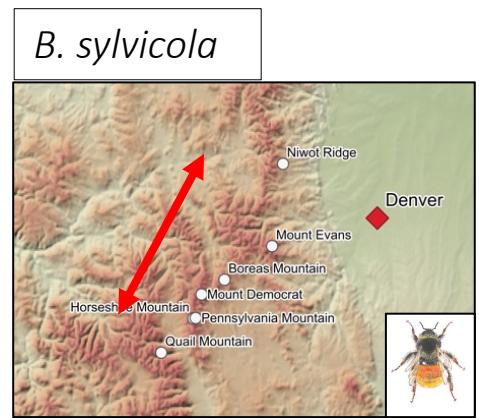
# Islands of divergence overlap regions of low recombination and centromeric repeats



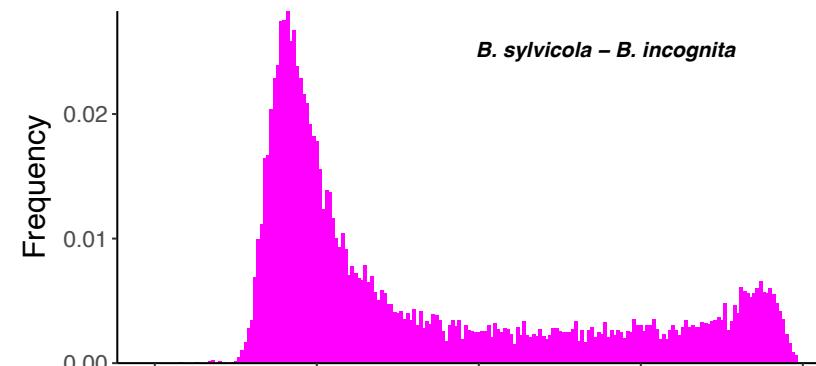
# Islands of divergence overlap regions of low recombination and centromeric repeats



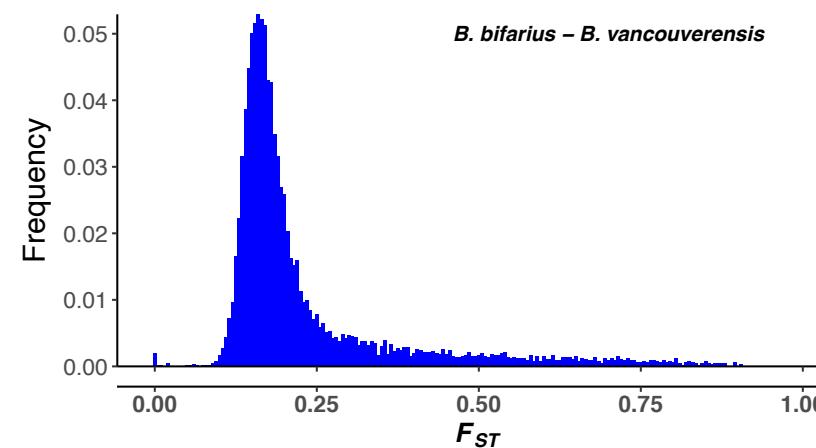
# $F_{ST}$ distribution is bimodal in sympatric, but not allopatric, comparison



within-species



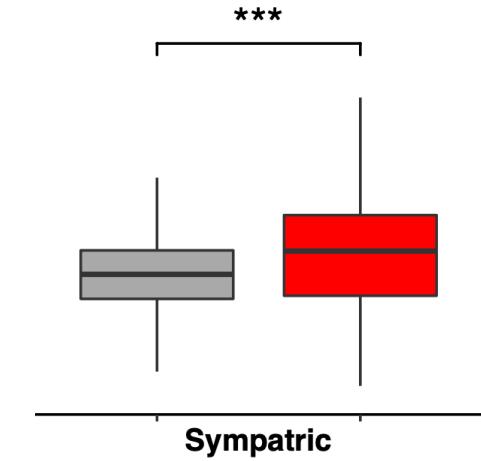
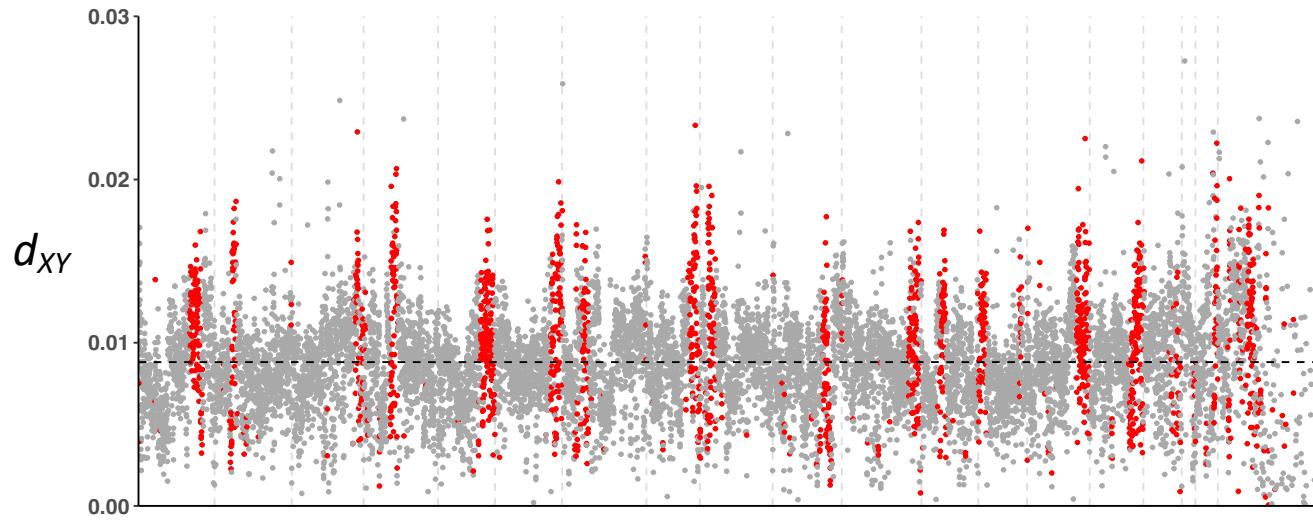
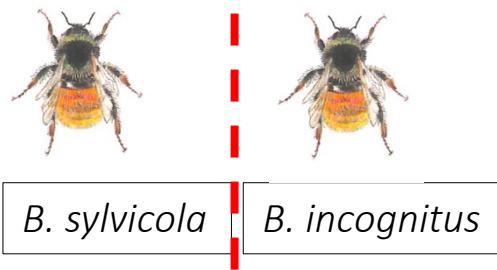
sympathy



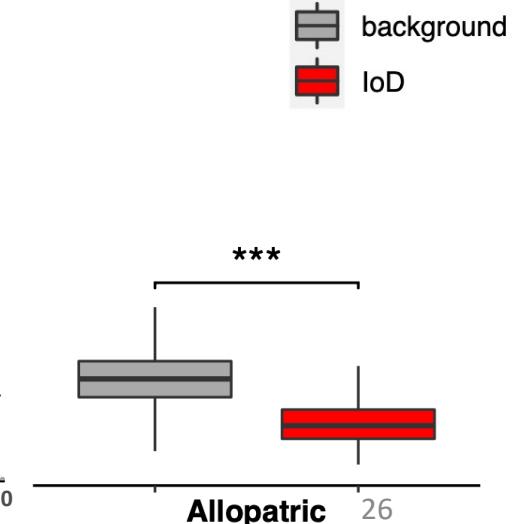
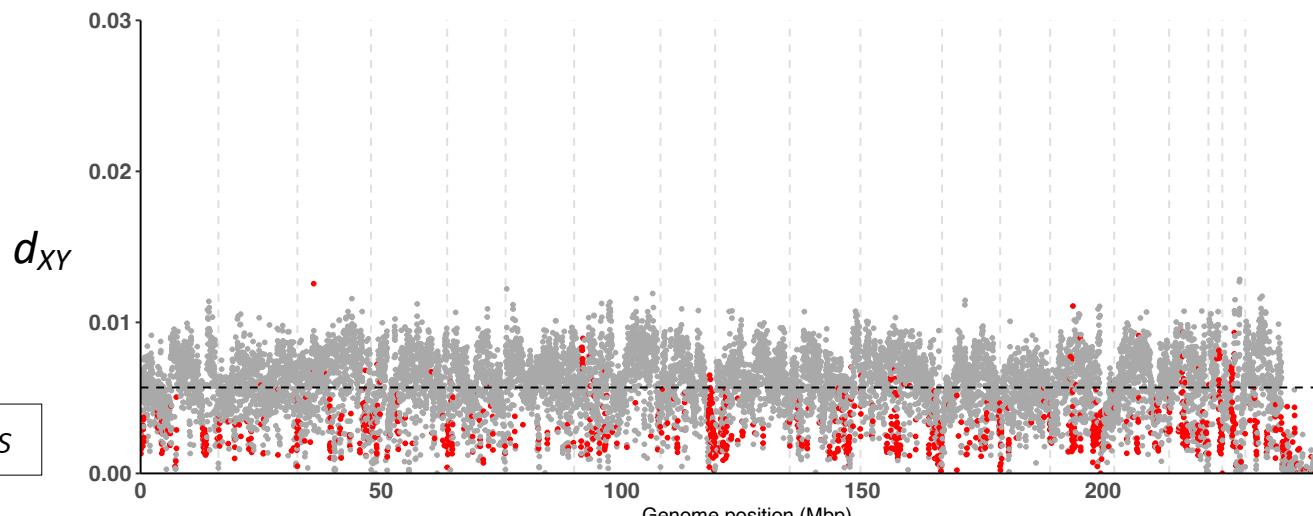
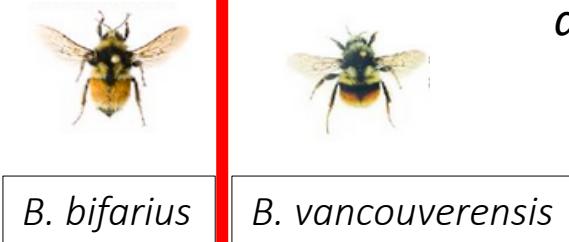
allopatry

$d_{XY}$  is elevated in islands of divergence in the sympatric, but not allopatric, comparison, indicating differential gene flow

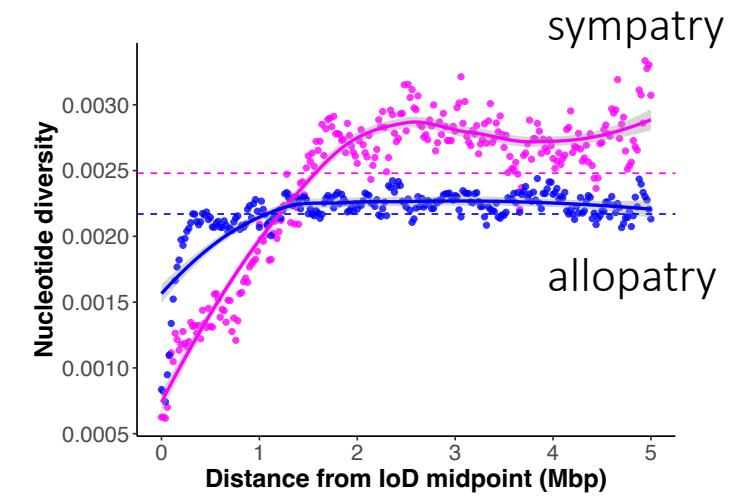
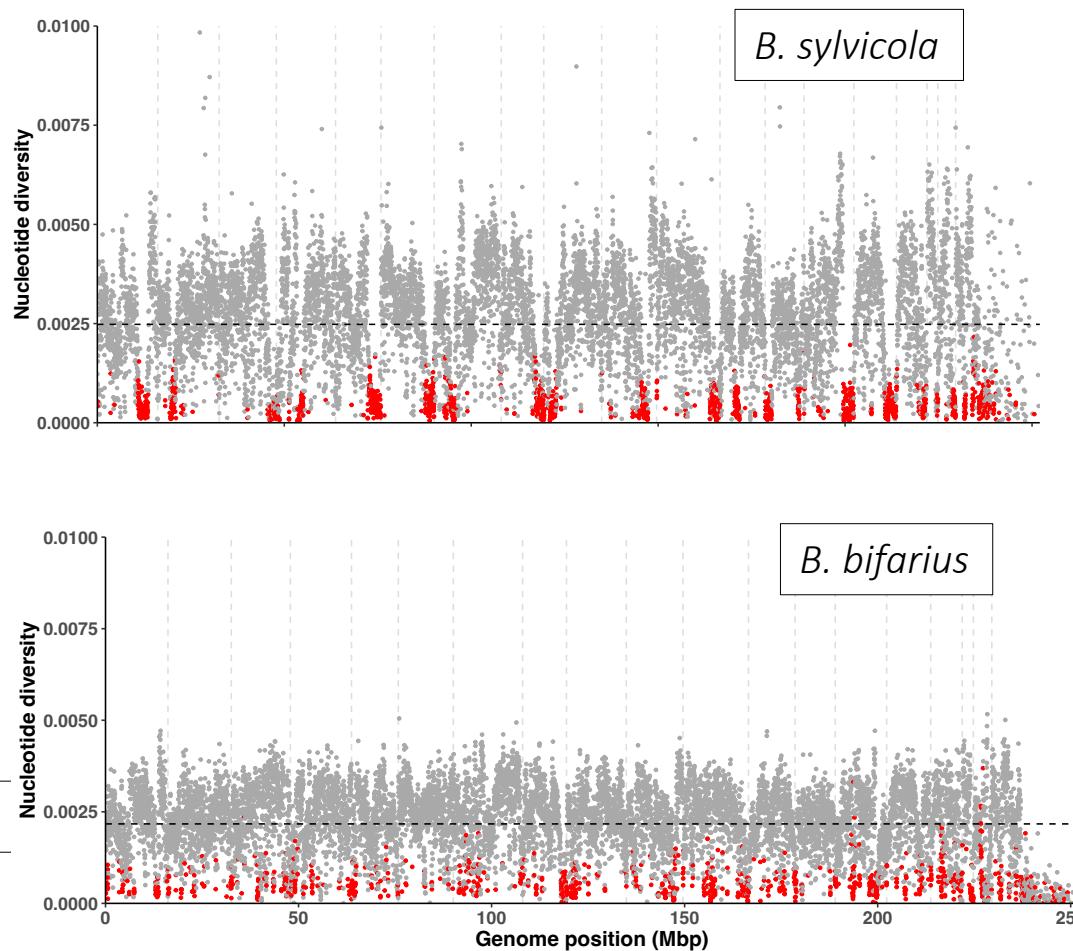
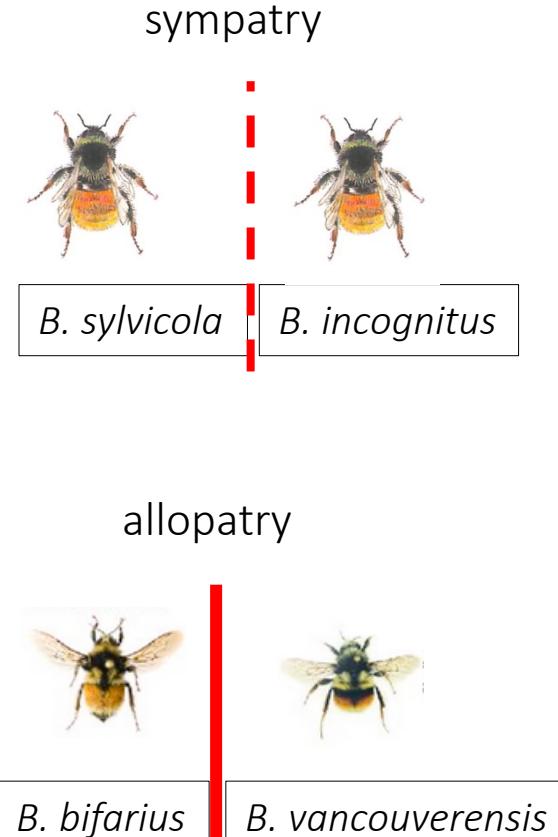
sympatry



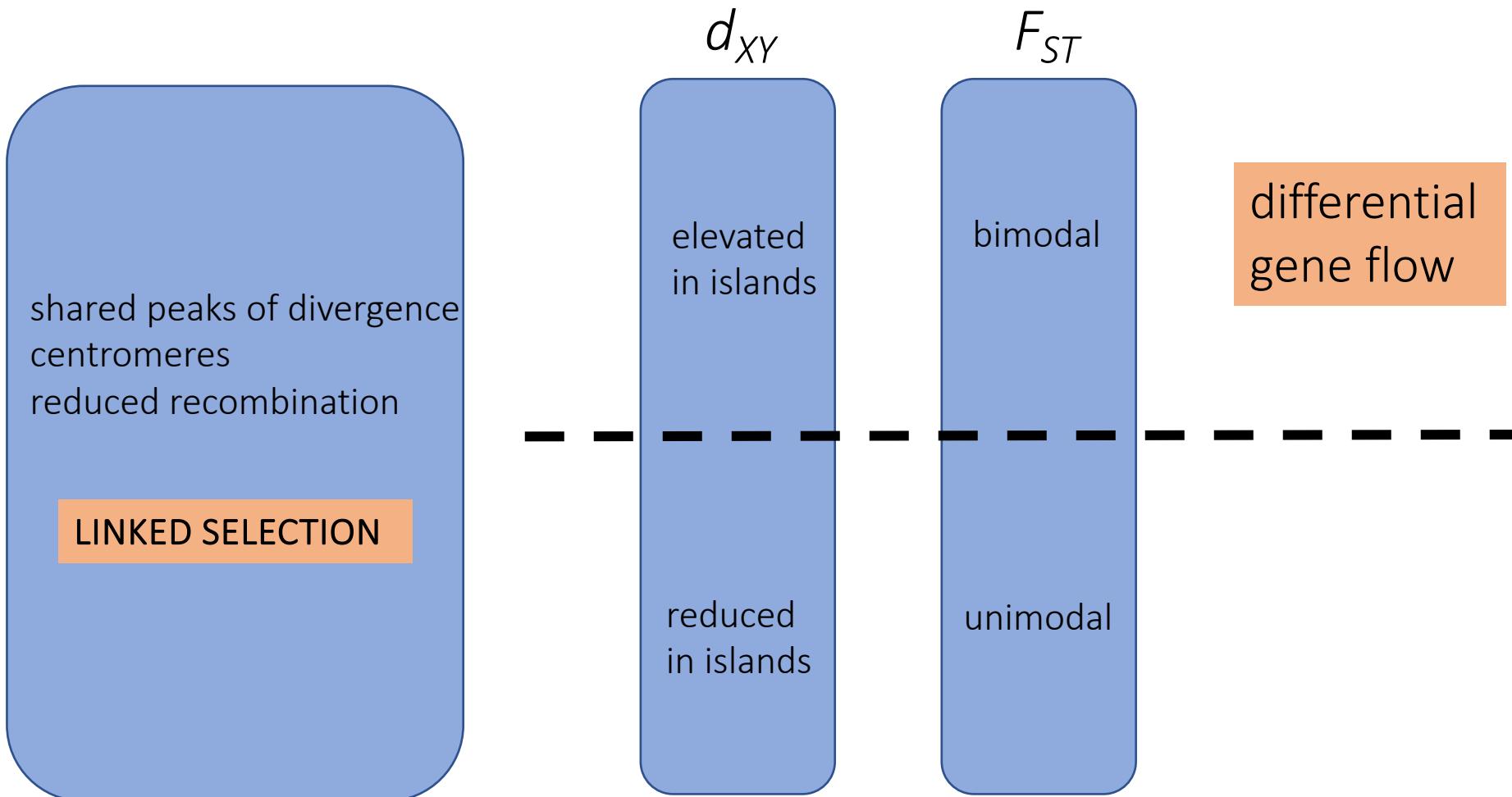
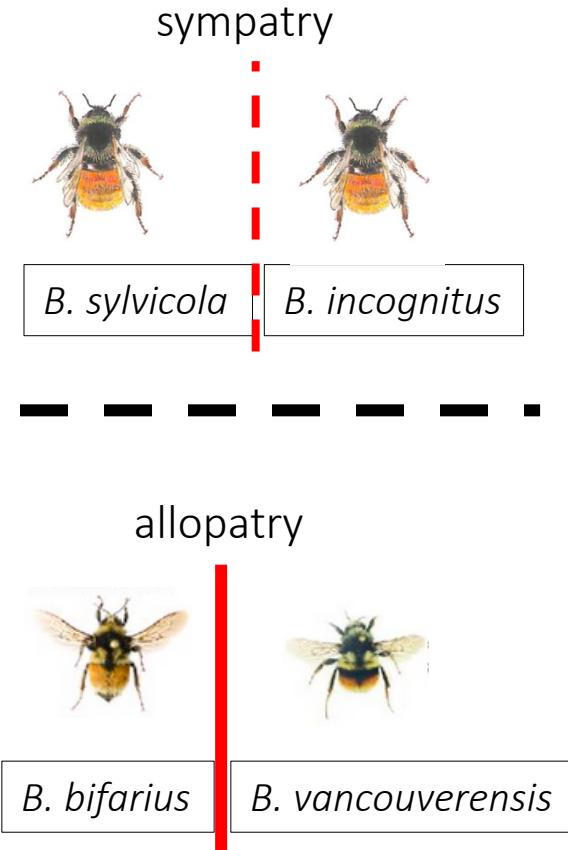
allopatry



# Extensive reduction in nucleotide diversity around islands of divergence in sympatry



# Genomic islands of divergence in sympatry and allopatry

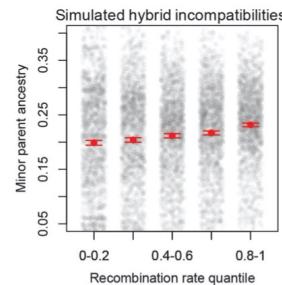
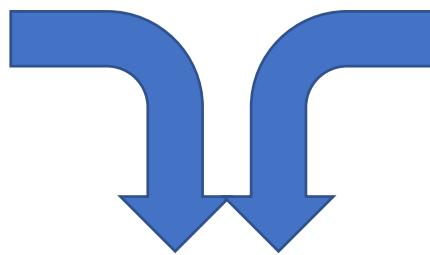


# Genomic landscape of divergence



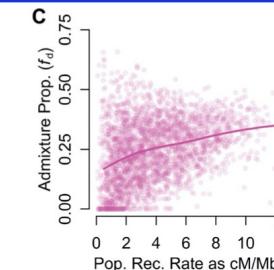
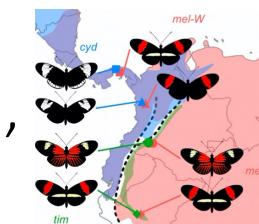
“Islands of speciation”  
resistant to gene flow

“Incidental islands”  
regions of low recombination,  
interaction with linked selection



Schumer et al. (2018) Science

Polygenic species barriers  
regions of low recombination,  
resistant to gene flow



Martin et al. (2019) PLoS Biol

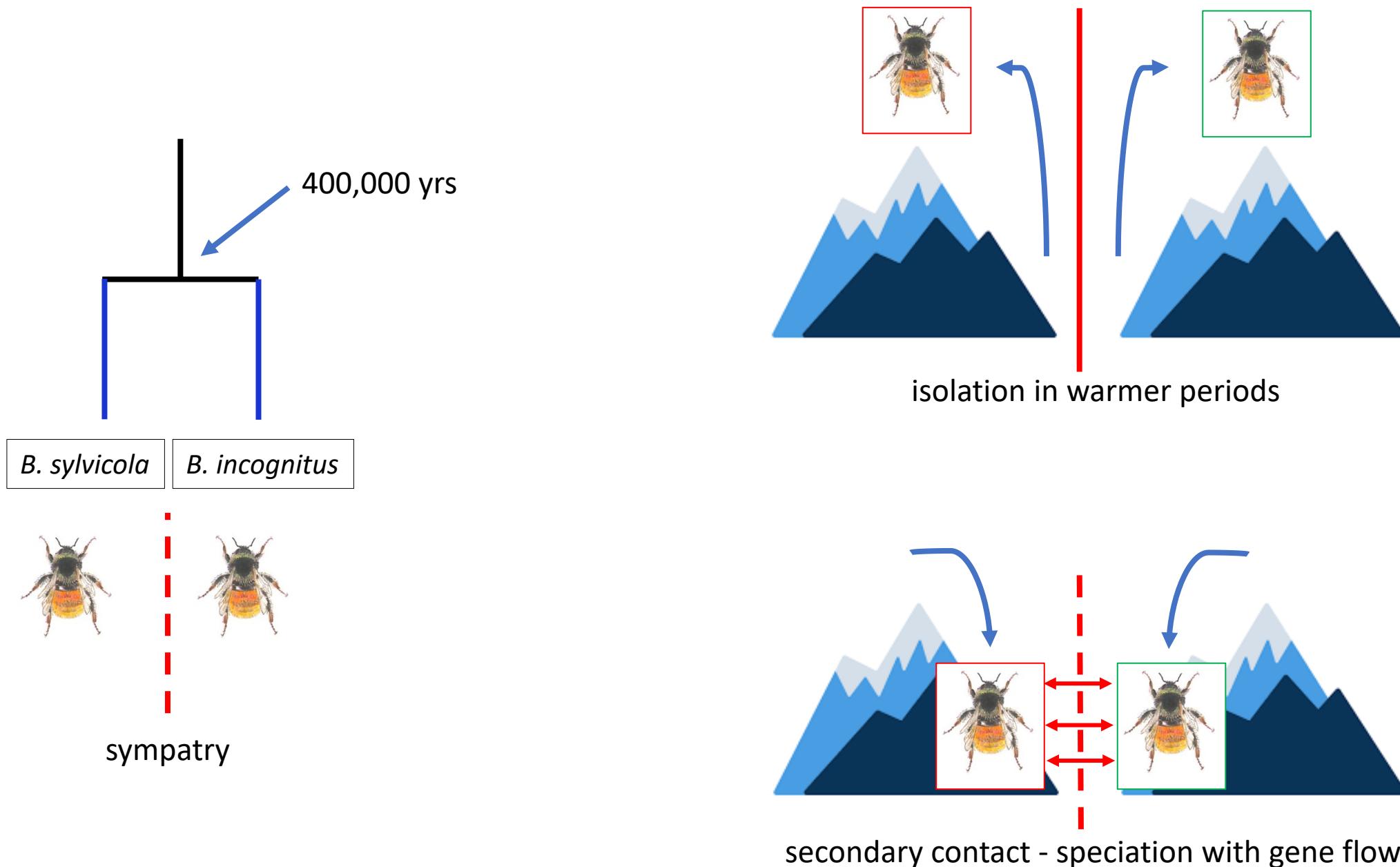
# Summary: Speciation with gene flow



Barriers to gene flow accumulated in:  
*regions of low recombination and near centromeres*

- Genomic incompatibilities may be widespread and polygenic
- In mountain bumblebees, warm periods may cause periods of isolation at high altitude, followed by secondary contact

# Possible speciation scenario



# Cryptic species

- *B. incognitus* and *B. sylvicola* are genetically distinct with no evidence of interbreeding
- Previously-undetected from morphology or genetic barcoding

**Brazil dolphin is first new river species since 1918**



**Gentoo penguins: three hidden species discovered**

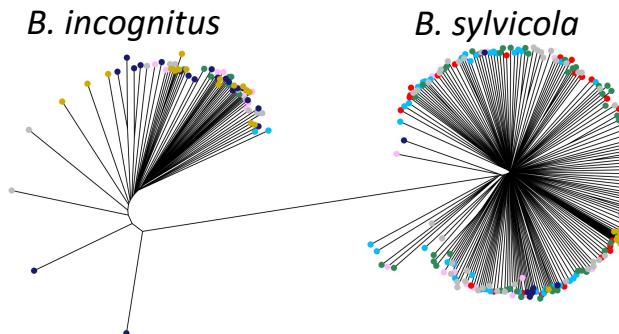
Genetics and body measurements reveal that four species of penguin have been masquerading as one...



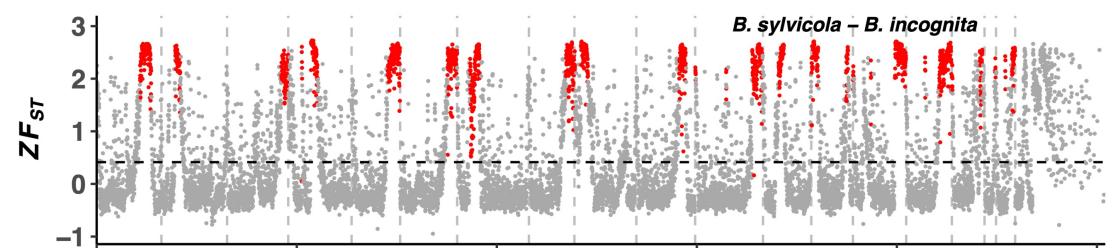
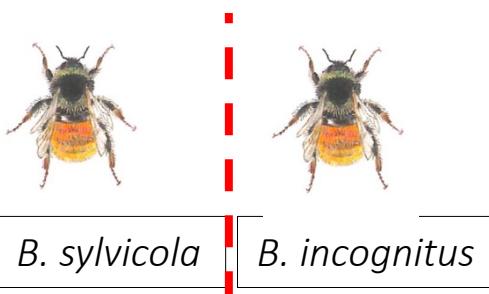
- How many more cryptic species?
- Is DNA evidence enough to define a new species?
- More resolution from genome sequencing compared to barcoding

# Conclusions

- Identification of cryptic species *Bombus incognitus*



- Speciation with gene flow
- Polygenic barriers to gene flow associated with centromeres



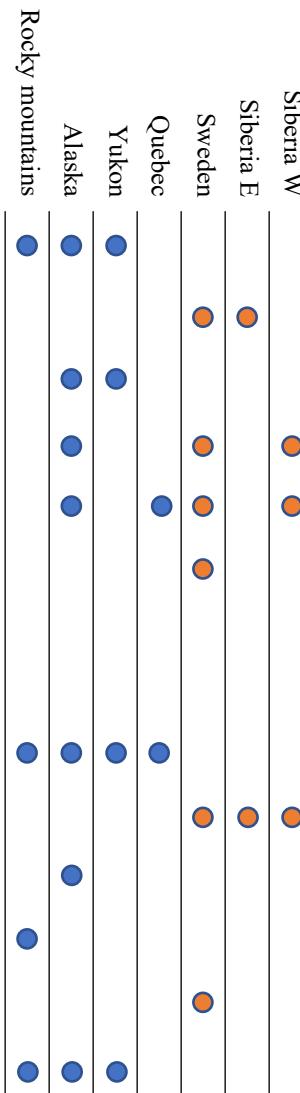
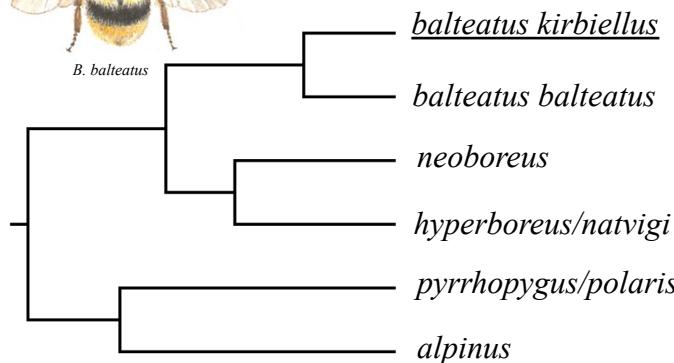
# Future Questions

a)

## Alpinobombus



*B. balteatus*

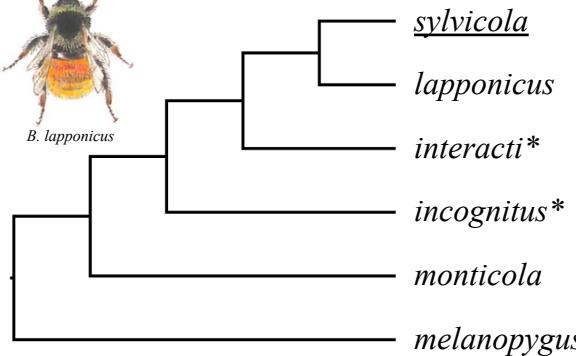


b)

## Pyrobombus



*B. lapponicus*



- Bombus incognitus?*
- More cryptic species?
- Can populations interbreed?
- Barriers to gene flow?
- Speciation mechanisms?
- Changes in genetic variation over time?
- Parallel genetic and morphological evolution across continents?

# Acknowledgements

**Matthew J. Christmas, Julia C. Jones, Anna Olsson, Ola Wallerman, Ignas Bunikis, Marcin Kierczak**

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*Uppsala University / UEA, UK*

Nicole E. Miller-Struttmann, Jennifer C. Geib,

*Webster University / Appalachian State University, USA*

**SciLifeLab**

