

Population genomics of arctic and montane bumblebees



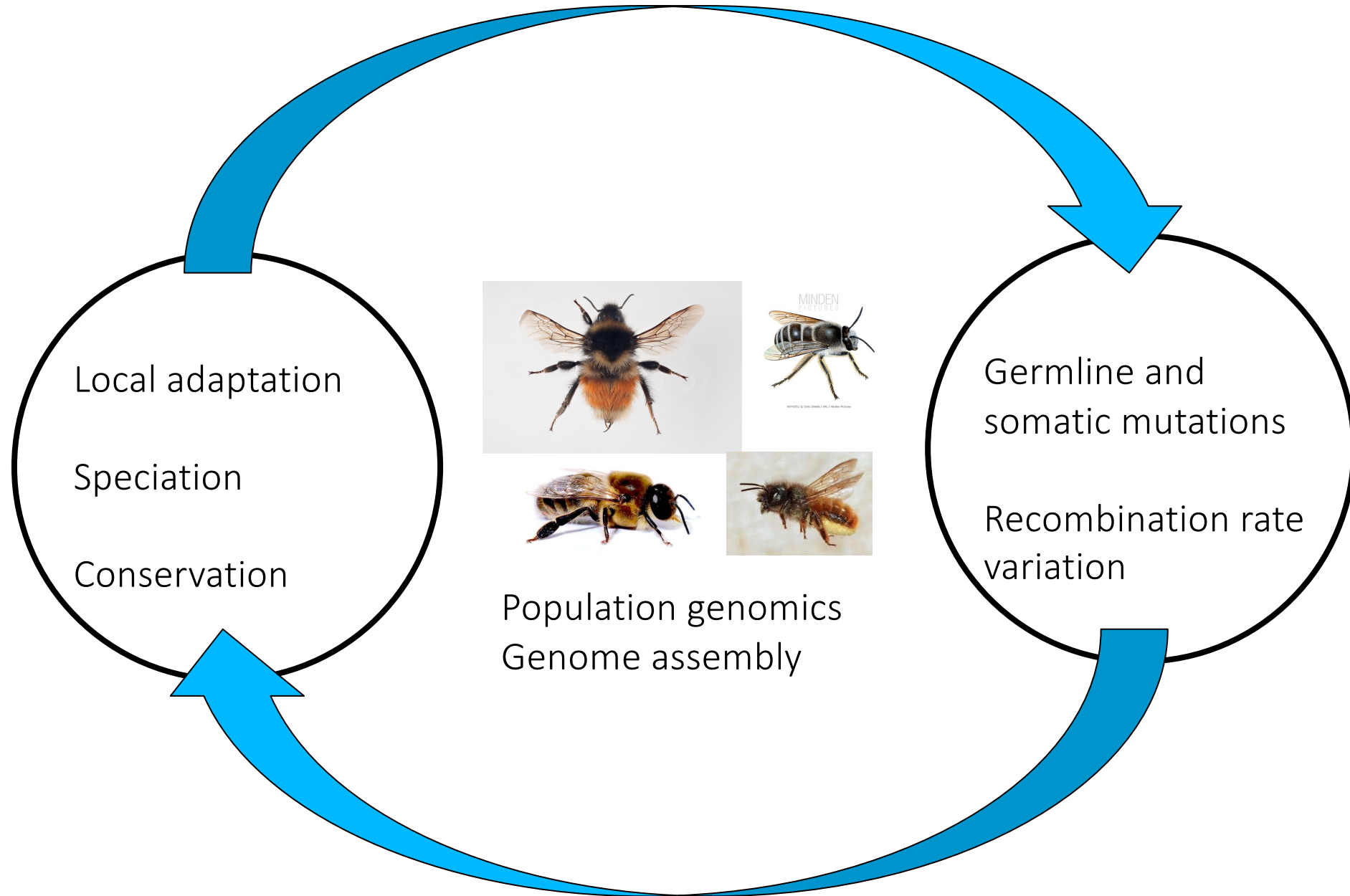
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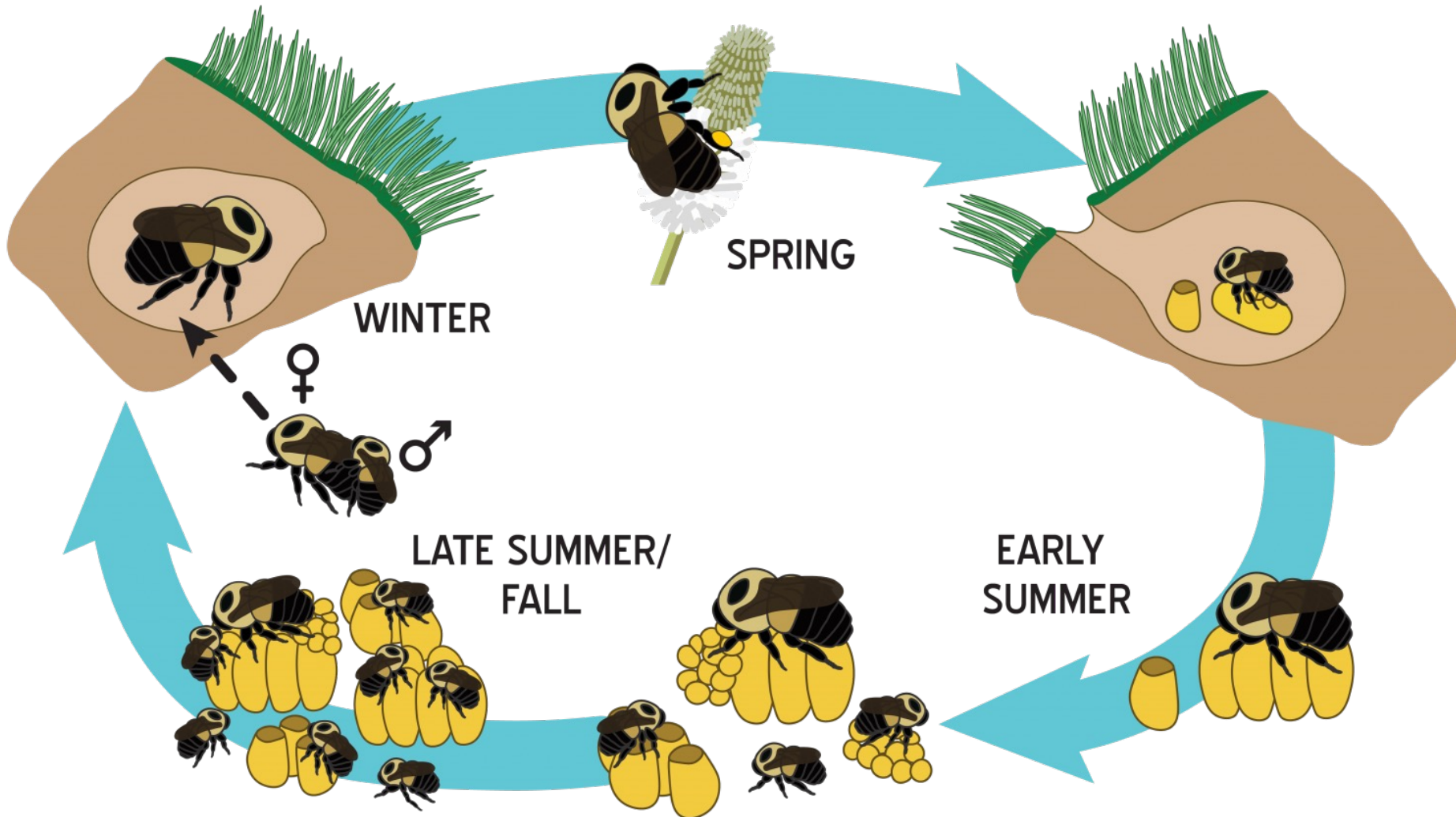
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SciLifeLab



Bumble bees



worker
queen

males

diploid
2n

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

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

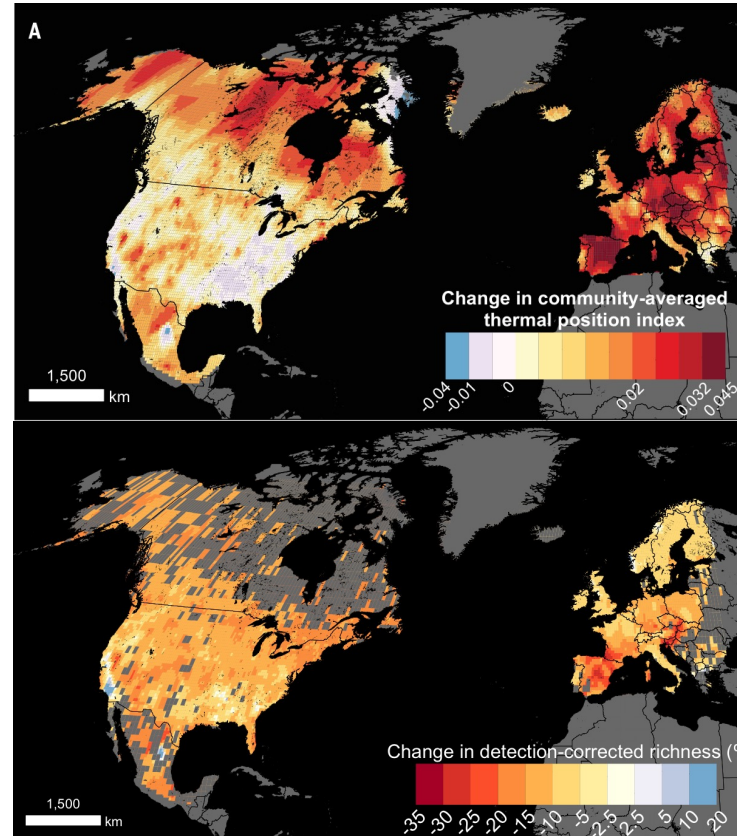
POLLINATOR DECLINE

Climate change contributes to widespread declines among bumble bees across continents

Peter Soroye^{1*}, Tim Newbold², Jeremy Kerr¹

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.

Science (2020) 367, 685-688



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

Denver

Mount Evans

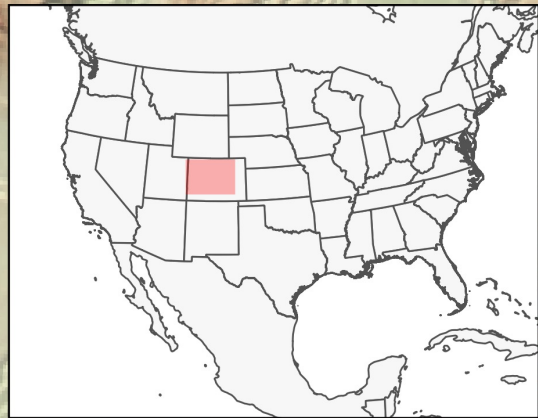
Boreas Mountain

Mount Democrat

Horseshoe Mountain

Pennsylvania Mountain

Quail Mountain



0 50 100 km



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

Bioinformatics

Nanopore assembly: wtdbg2 + Racon + Medaka

10x error correction: LongRanger + Tigmint + Pilon

10x scaffolding: ARCS + LINKS

Annotation pipeline: StringTie + MAKER

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%



B. balteatus



B. sylvicola

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) [†]	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

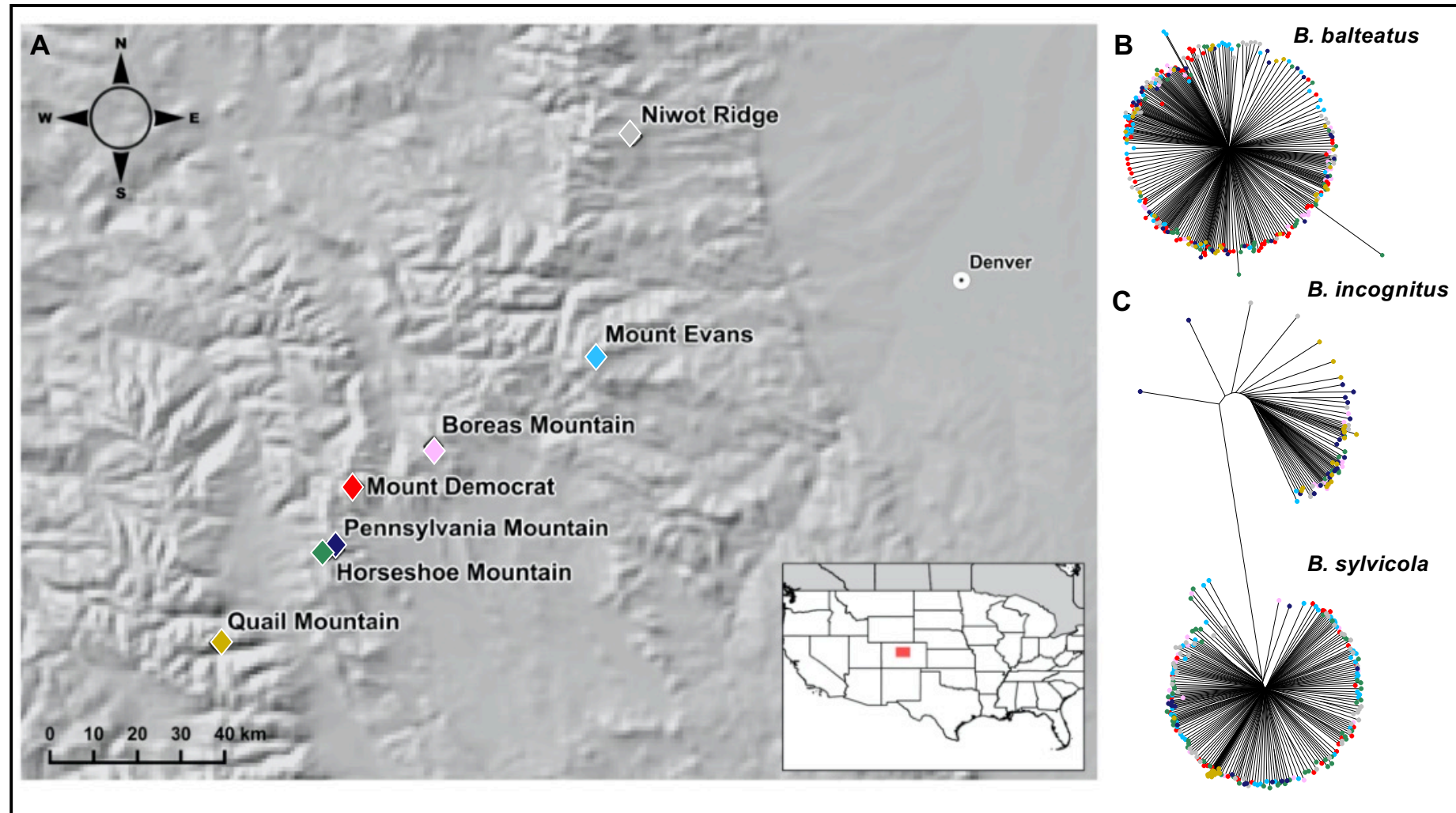
*BUSCO analysis using the OrthoDB v. 10, Hymenoptera dataset.

[†] Numbers in brackets represent total ungapped length

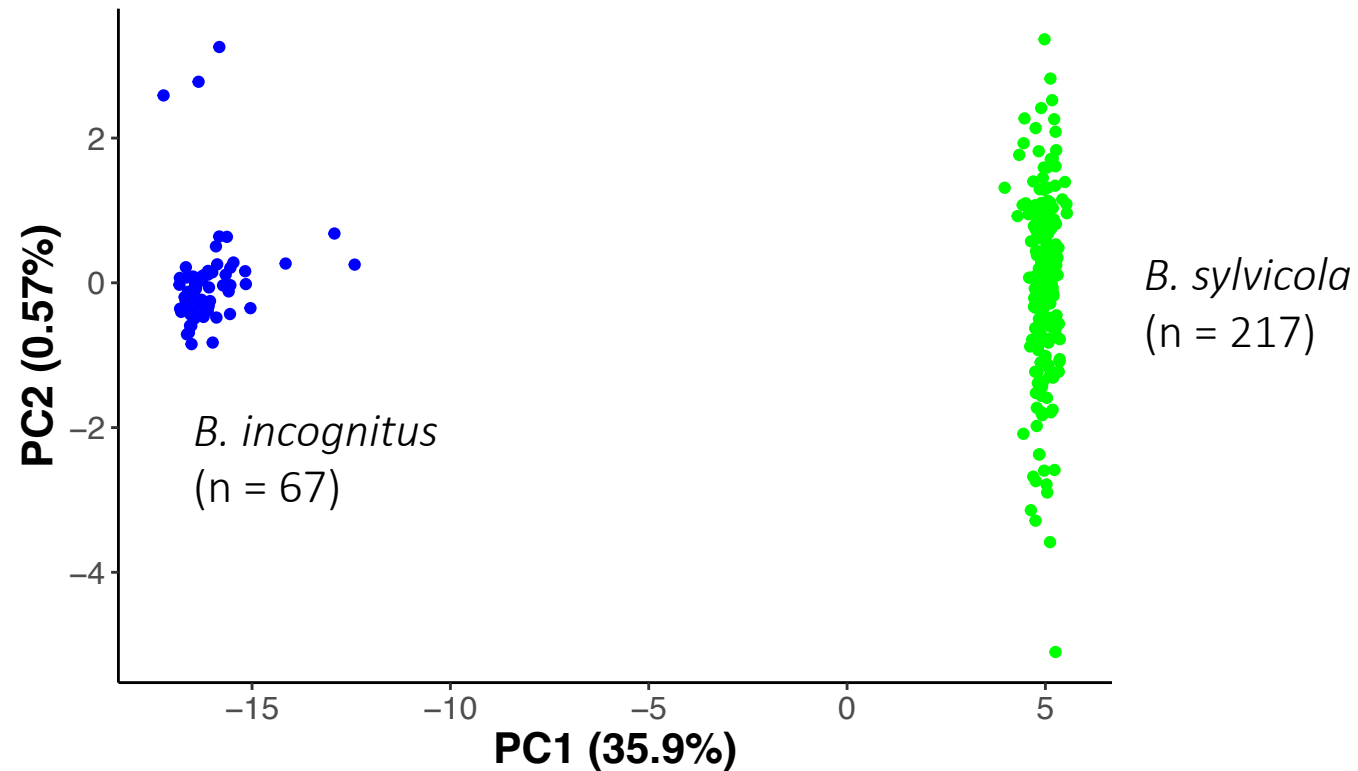
650 whole genome sequences of *B. sylvicola* and *B. balteatus*

Nextera Flex + HiSeqX → mean coverage ~15x

Not 2, but 3 species...



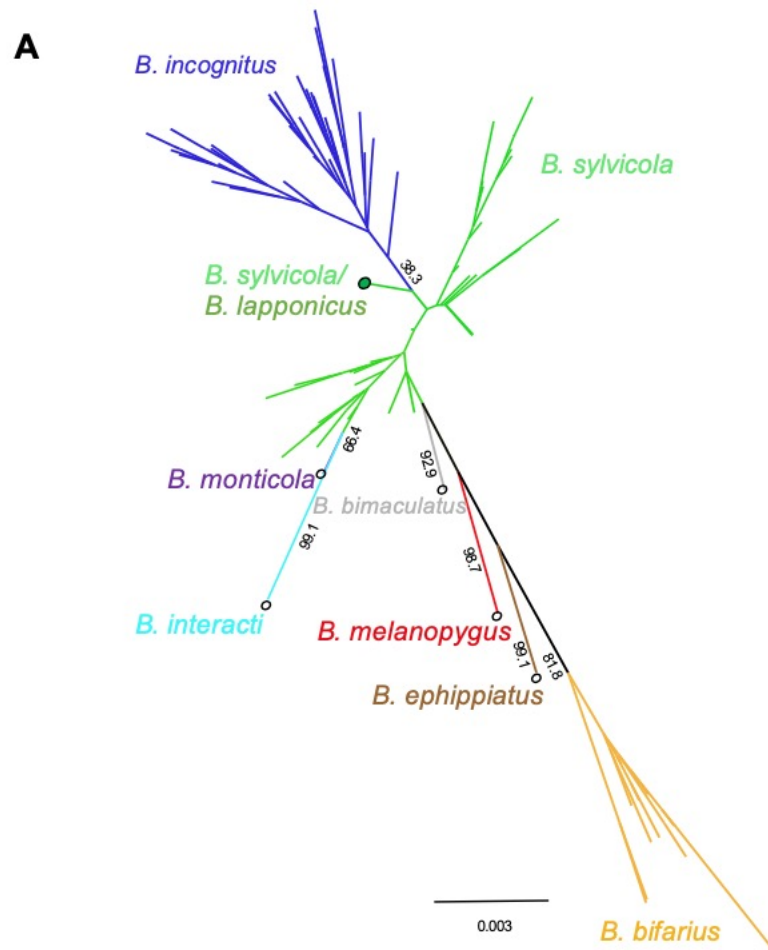
Clustering of sequences indicates presence of new cryptic species, *Bombus incognitus**



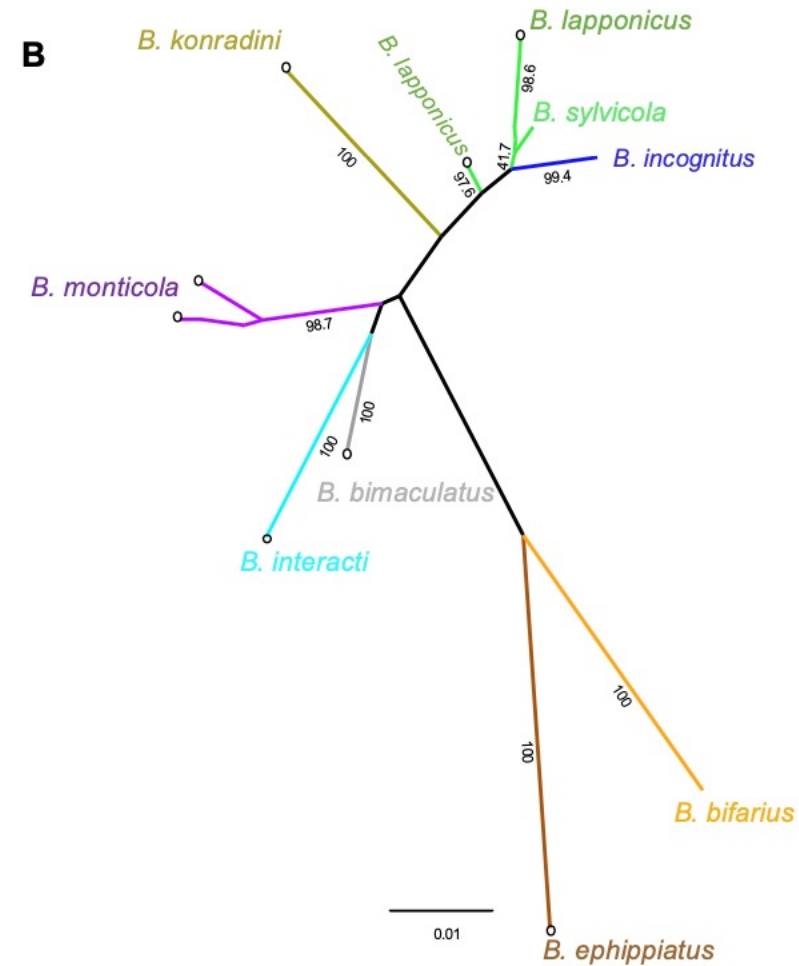
****not official name...***

- 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

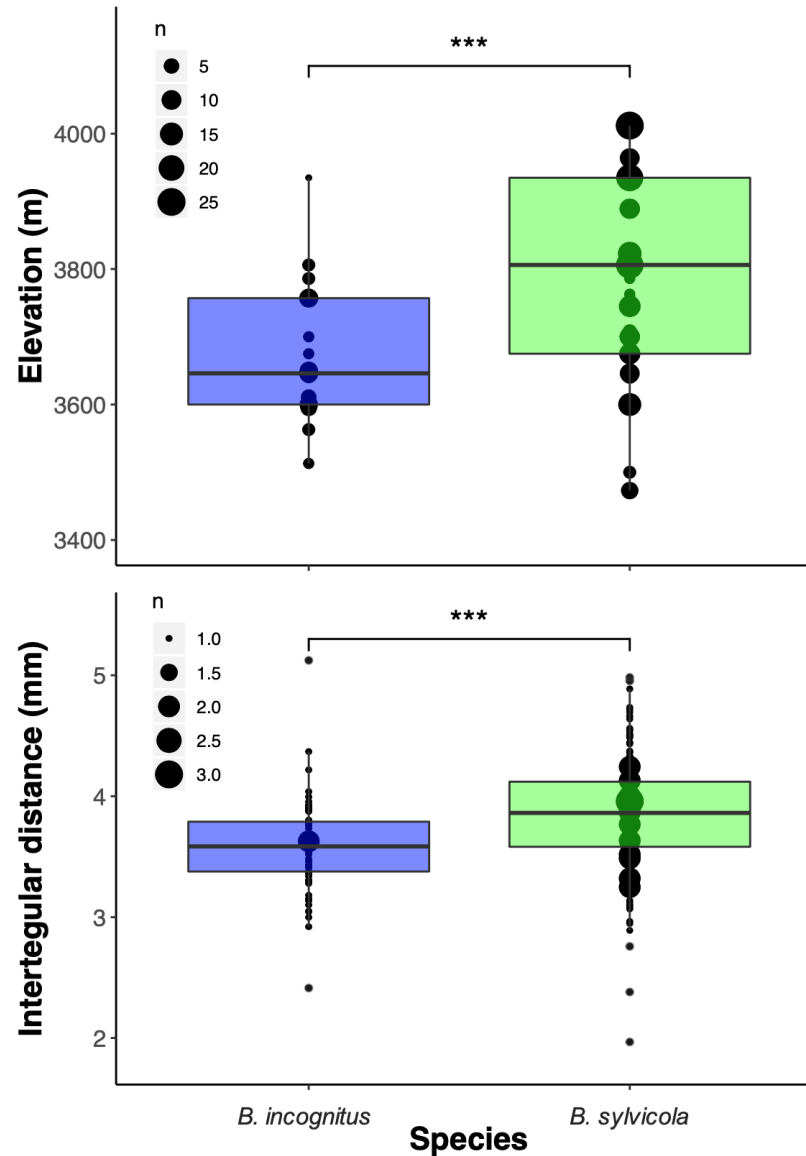


PEPCK gene



COXI

Bombus incognitus tends to be smaller and found at lower elevation

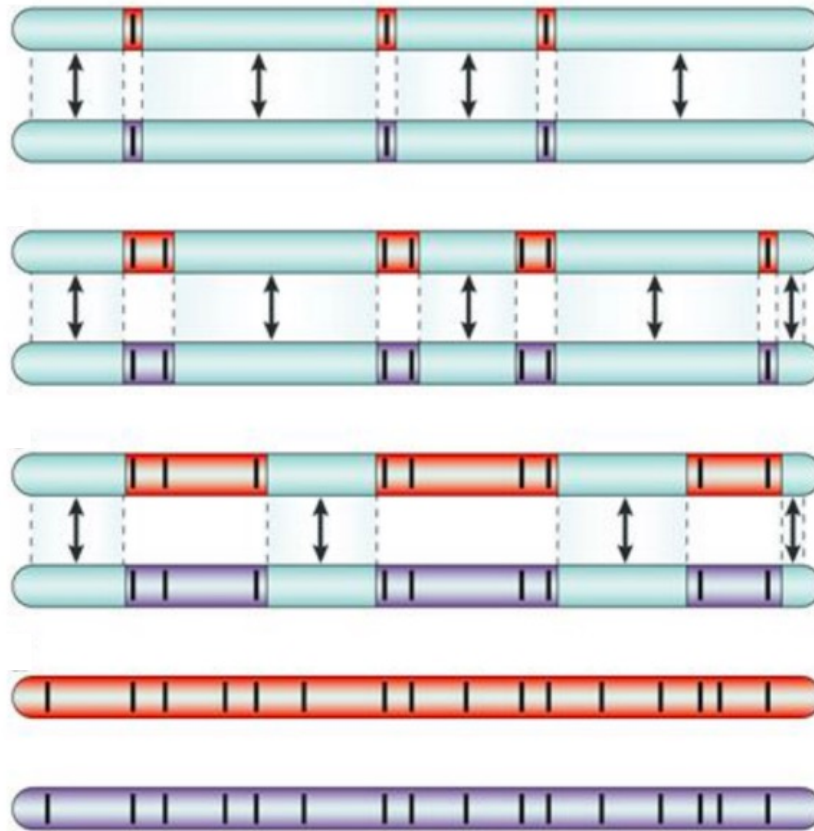


Speciation with gene flow

early divergence



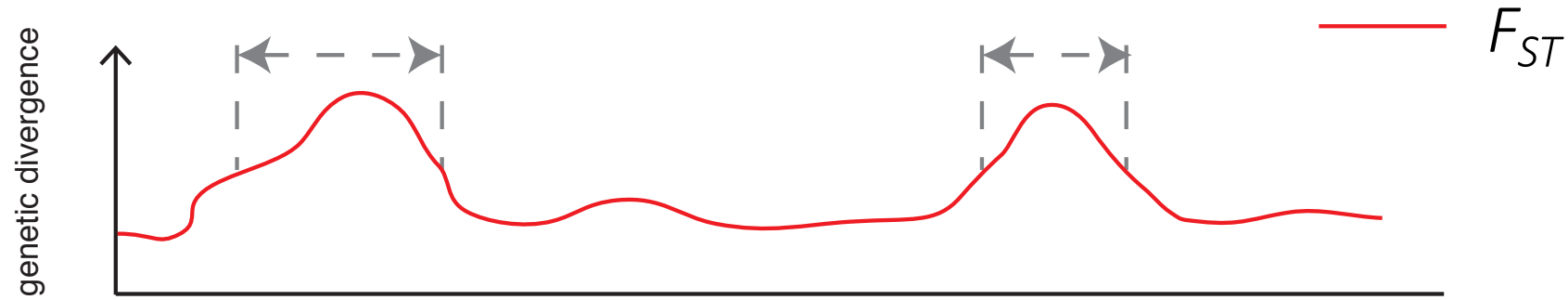
late divergence



“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

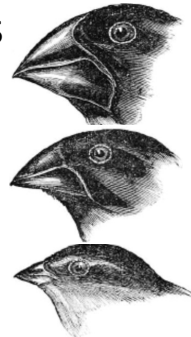
“Incidental islands”
regions of low recombination,
interaction with linked selection

genomic incompatibilities

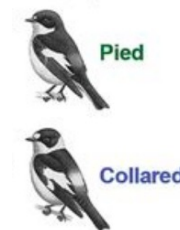
ecological specialization



Swordtail fish
Powell *et al.* (2020) Science

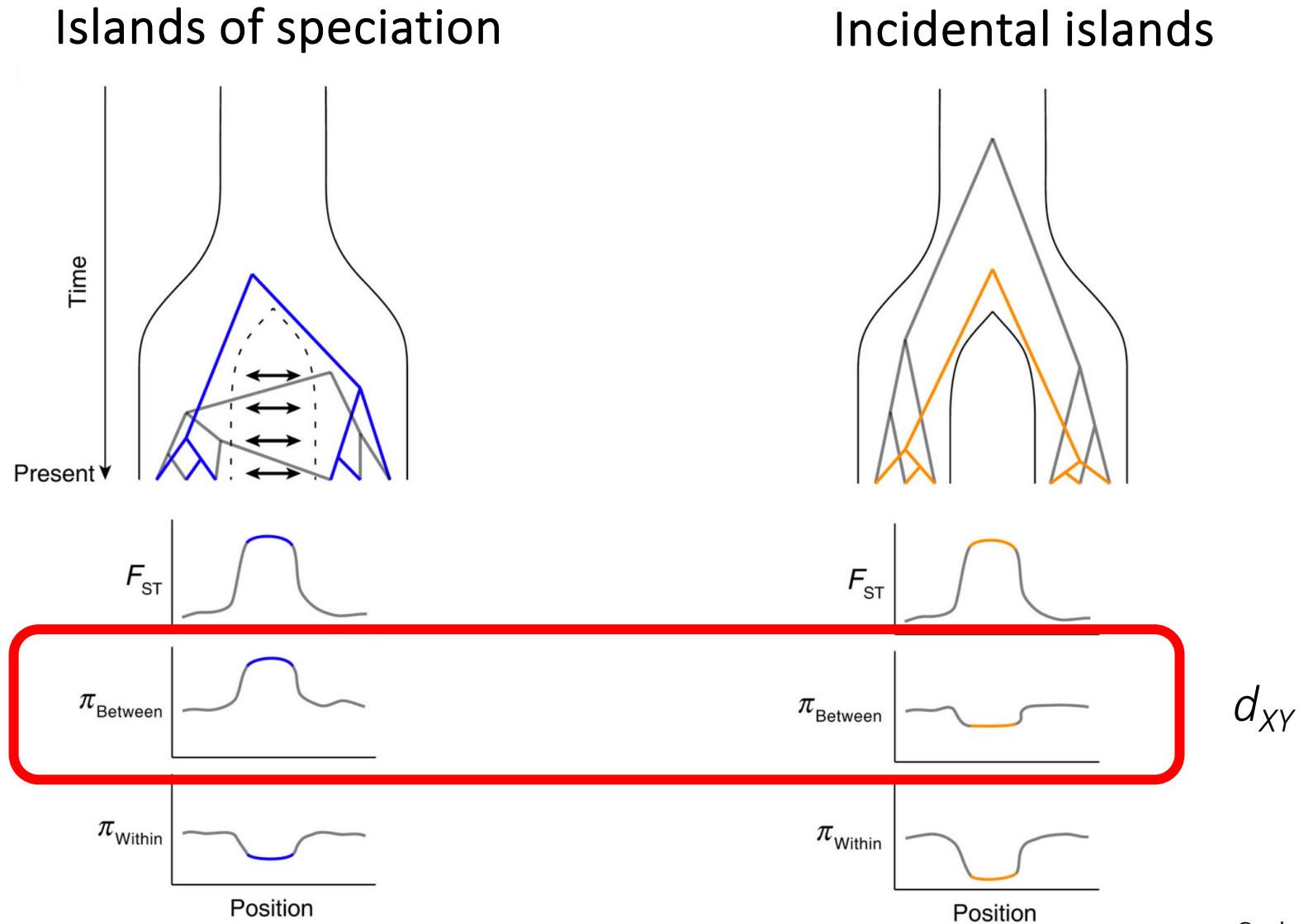


Darwin's finches
Han *et al.* (2017) Genome Res
Lamichhaney *et al.* (2015)
Nature

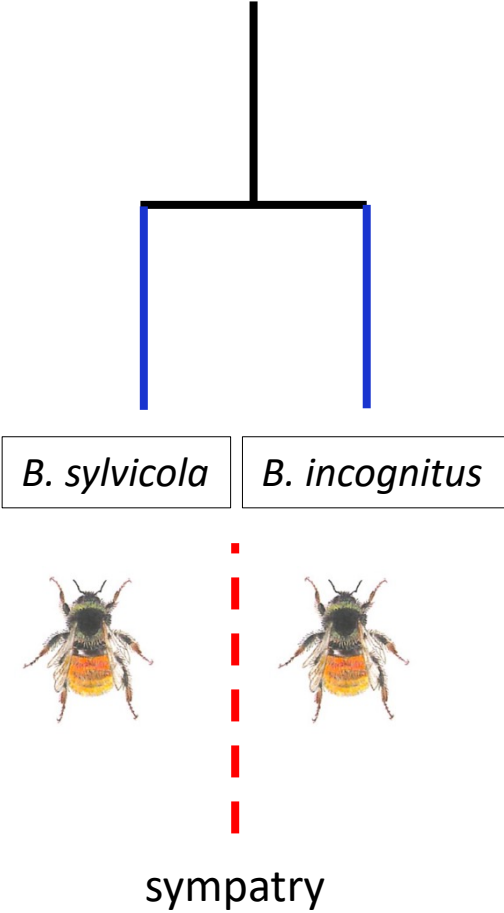
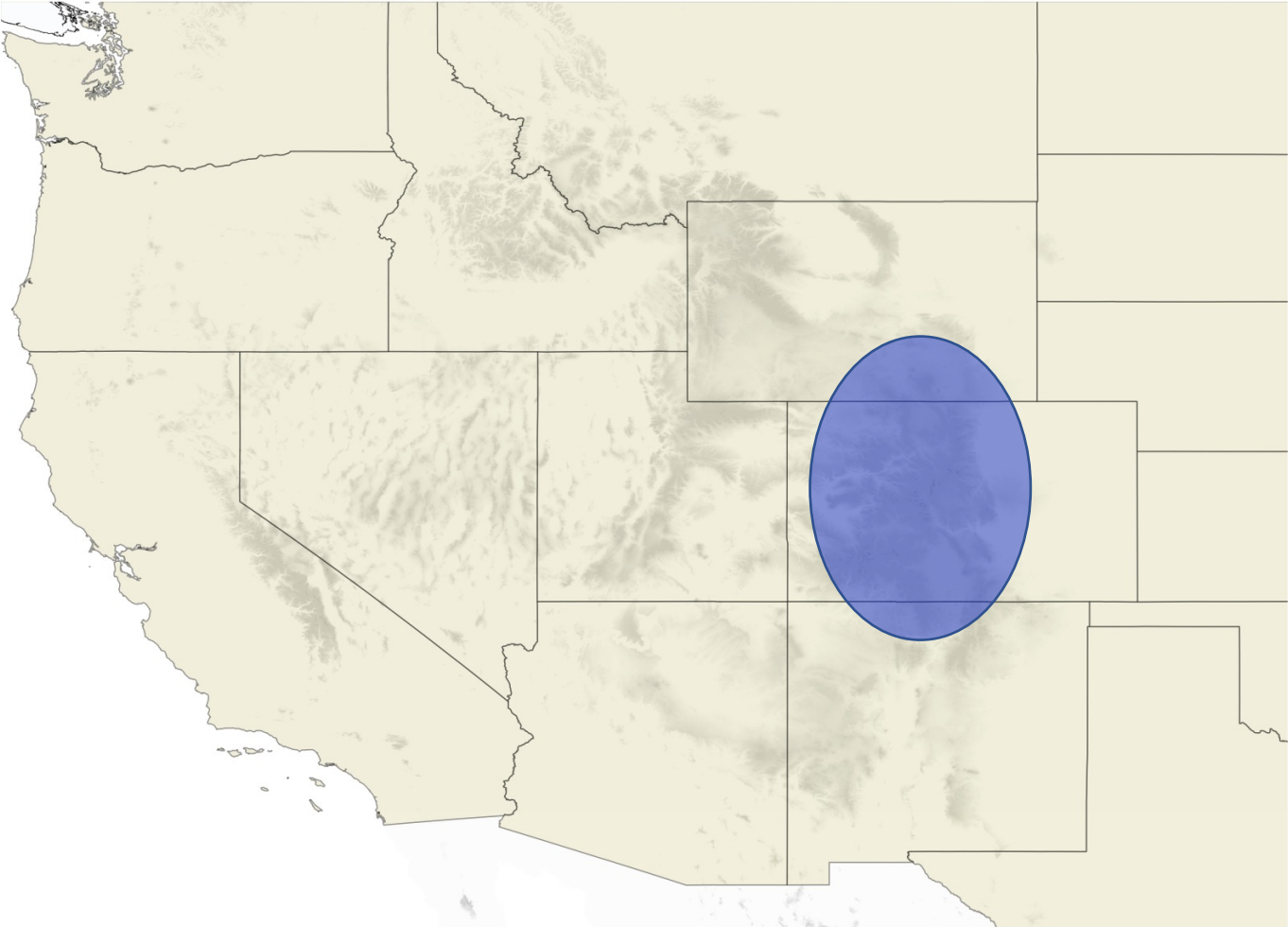


Burri *et al.* (2015) Genome Res.
Feulner *et al.* (2015) PLoS Genet.
Vijay *et al.* (2016) Nat. Commun.
Cruickshank & Hahn (2014) Mol Ecol

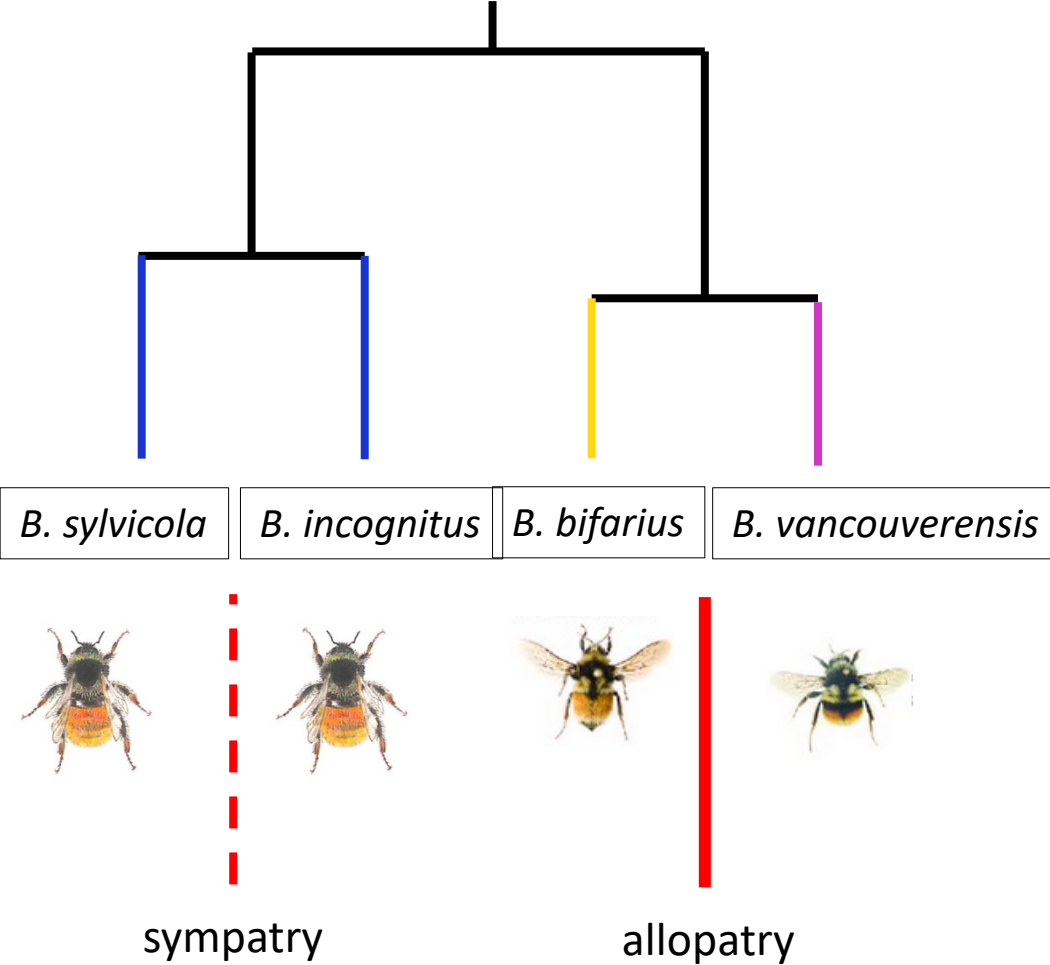
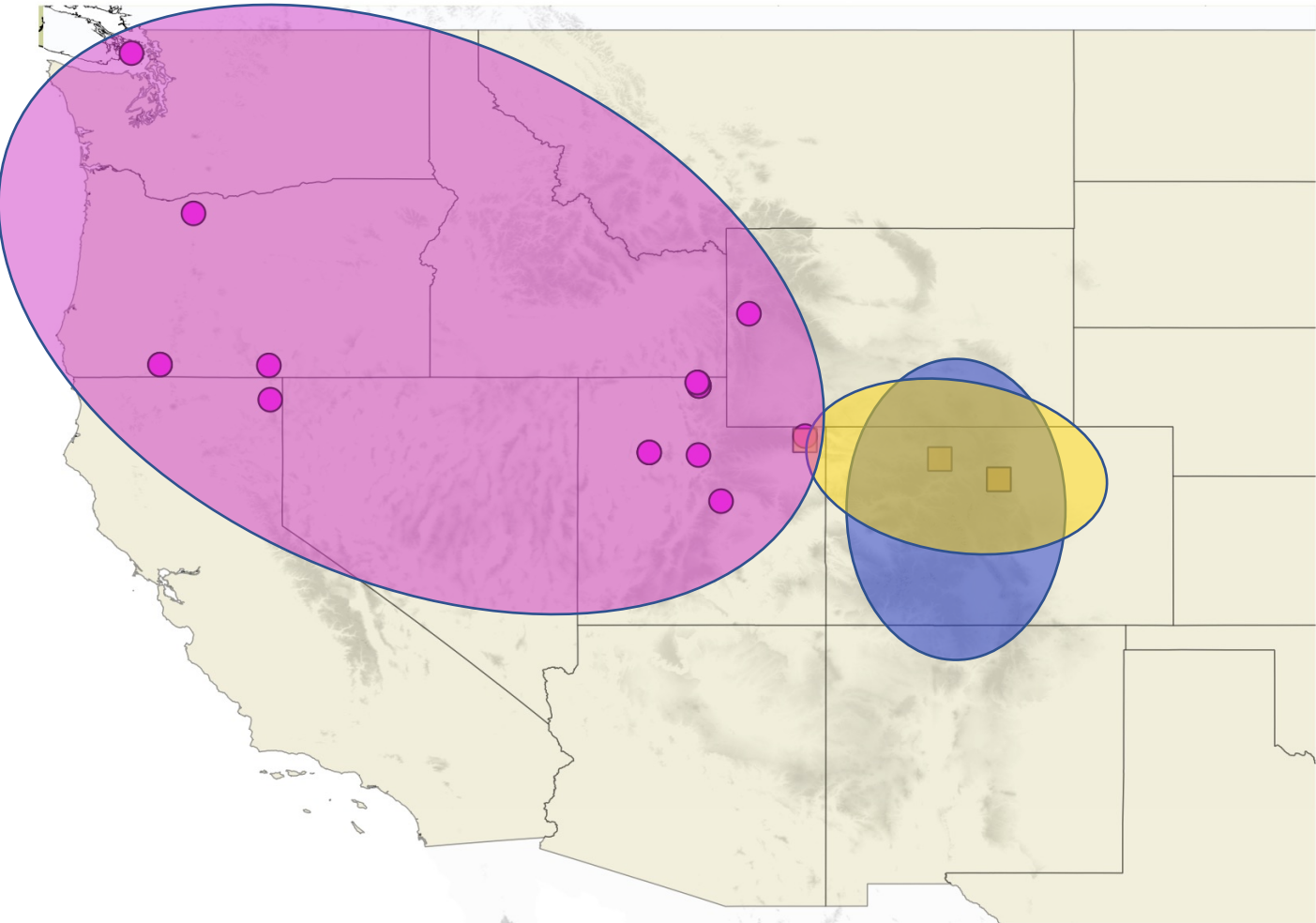
Absolute divergence (d_{XY}) identifies differential gene flow



Comparison of genome divergence in sympatry and allopatry



Comparison of genome divergence in sympatry and allopatry



Sympatry

Allopatry

B. sylvicola
(n = 217)

B. bifarius (n = 21)

B. incognitus
(n = 67)

B. vancouverensis
(n = 17)

396,000 YBP

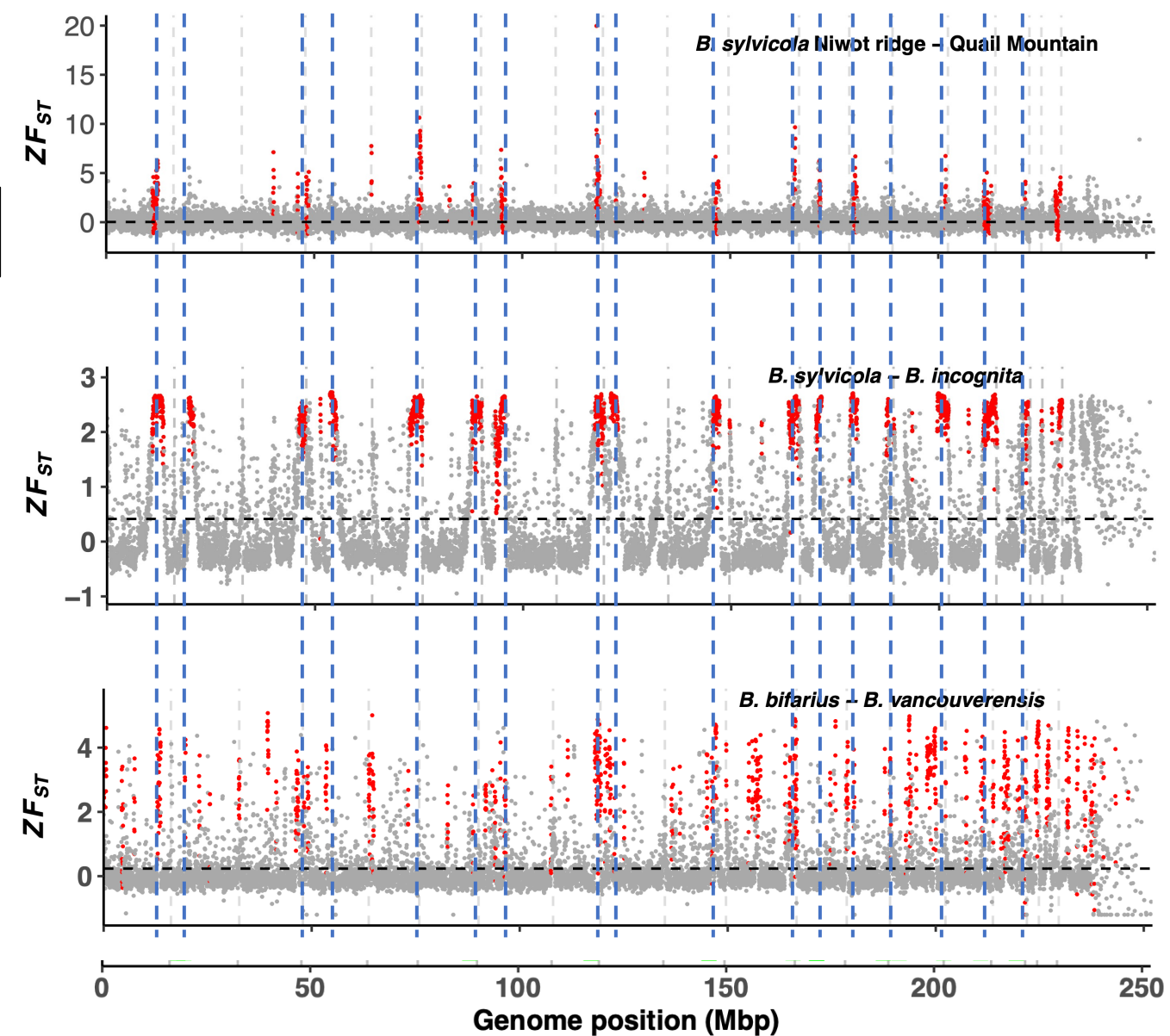
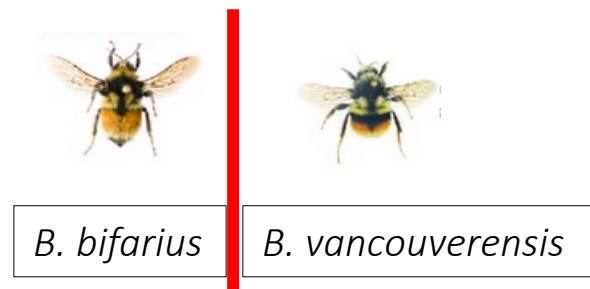
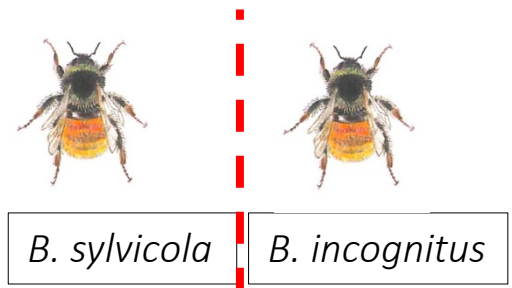
68,000 YBP

Species

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

Additional data from
Ghisbain et al. (2020) Syst. Entom.

Islands of divergence recur in the same genomic locations

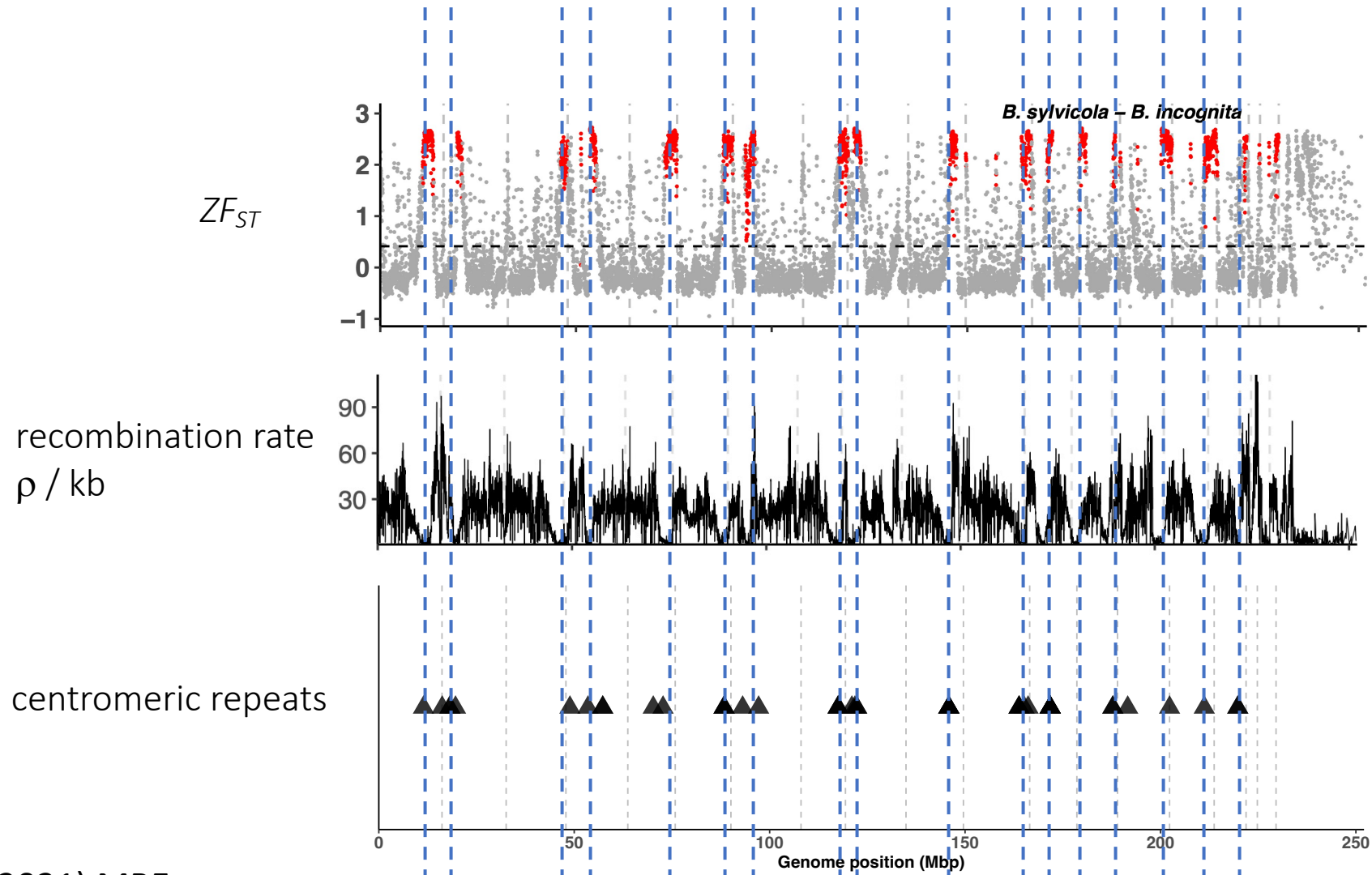


within species

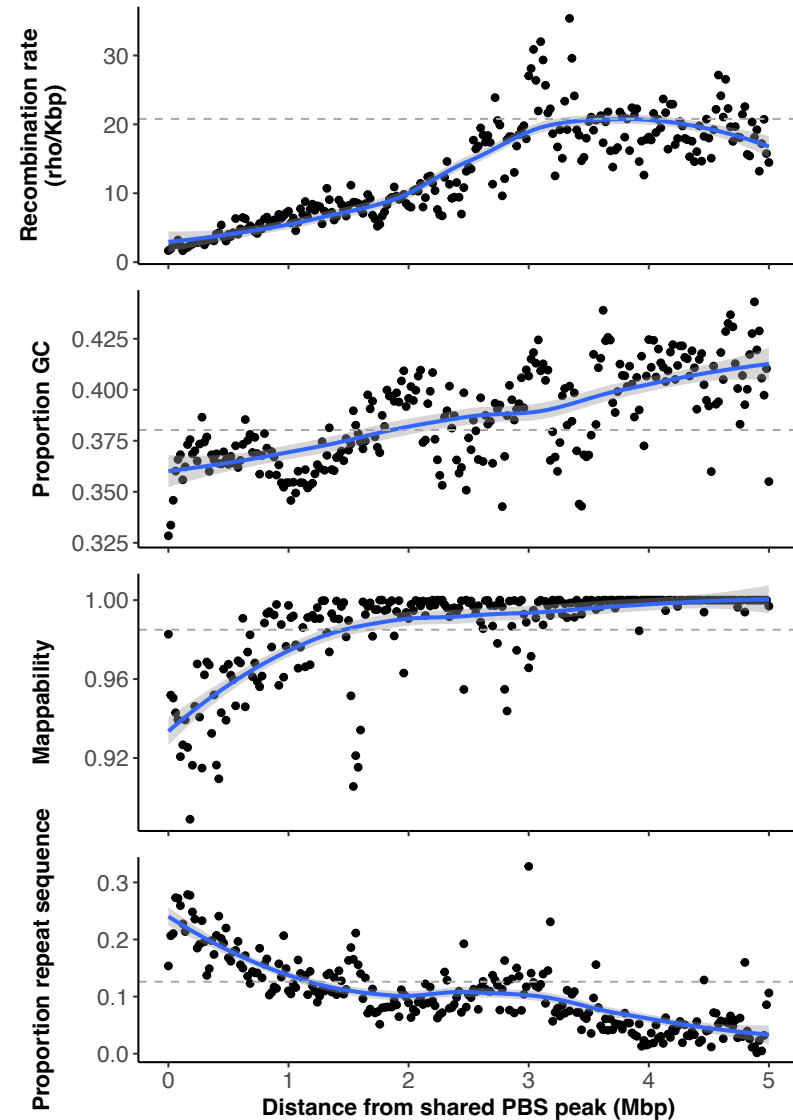
sympatry

allopatry

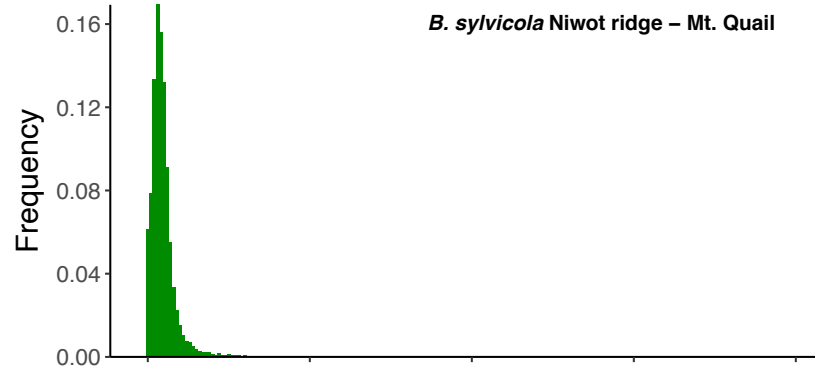
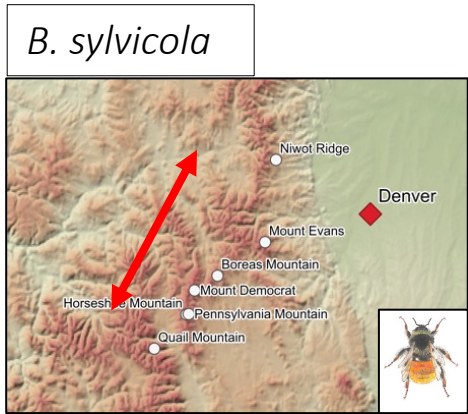
Islands of divergence overlap regions of low recombination and centromeric repeats



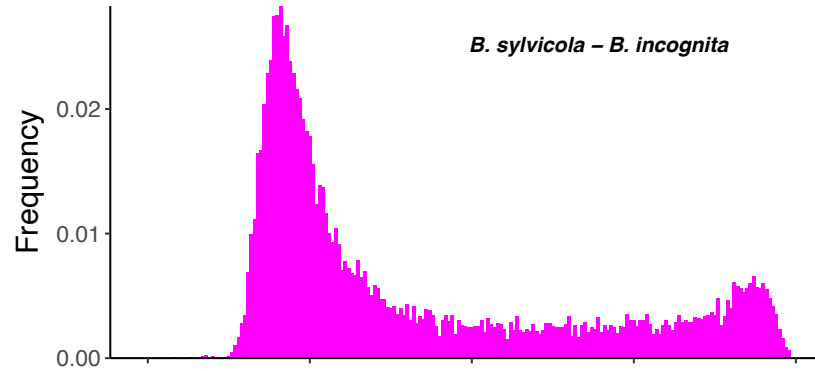
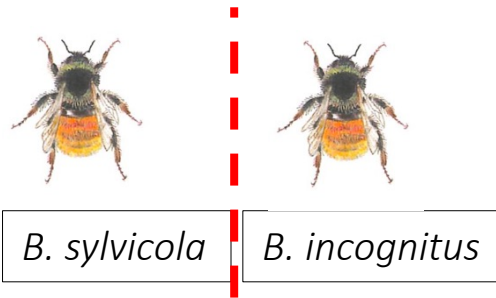
Islands of divergence overlap regions of low recombination and centromeric repeats



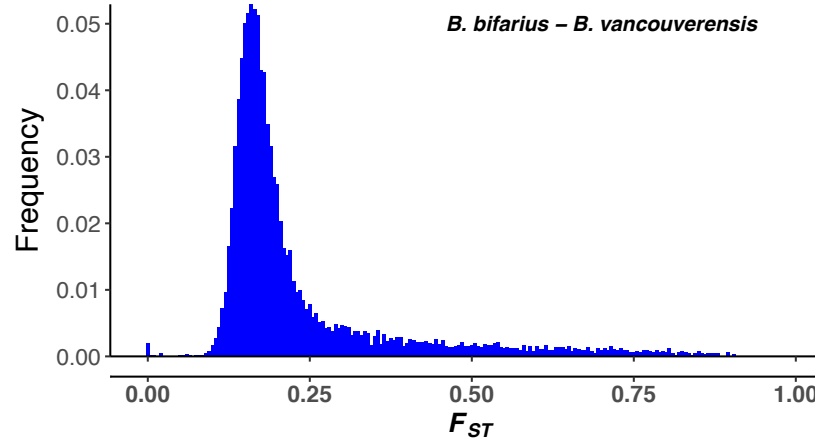
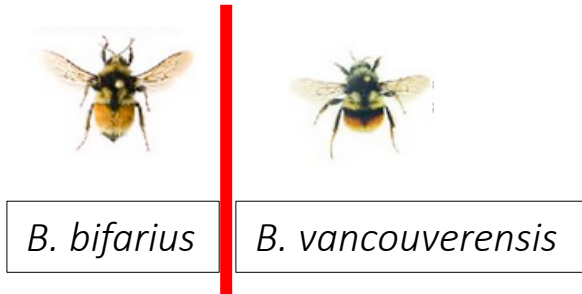
F_{ST} distribution is bimodal in sympatric, but not allopatric, comparison



within-species

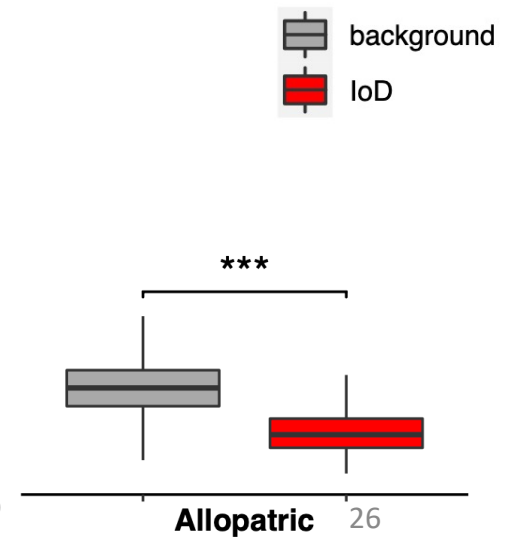
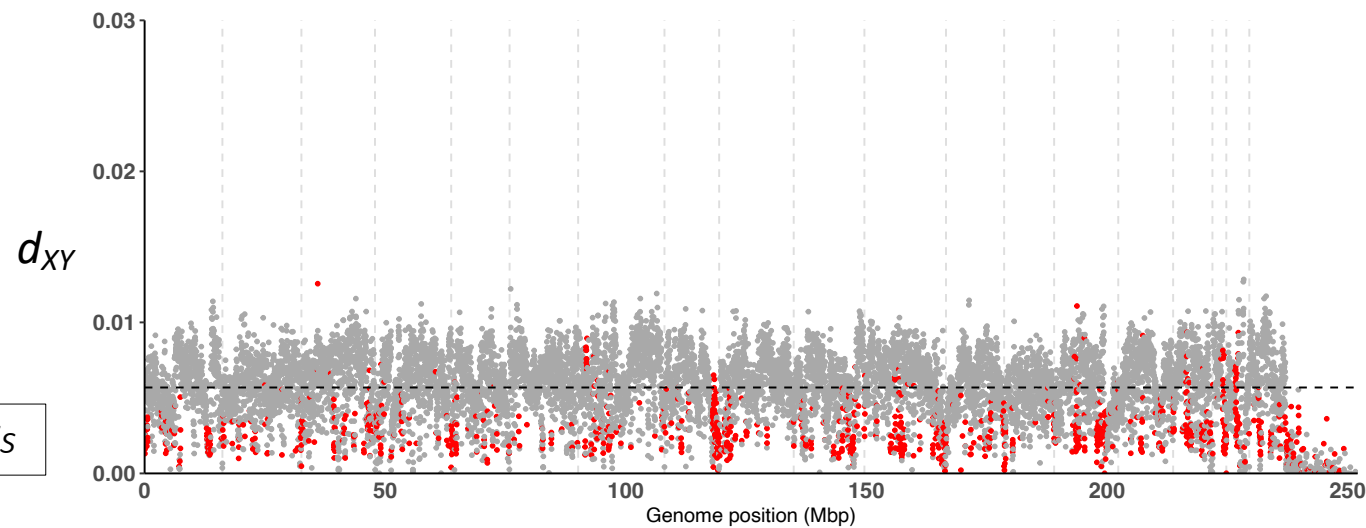
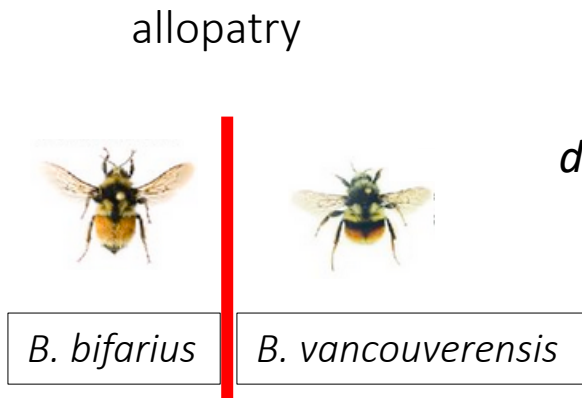
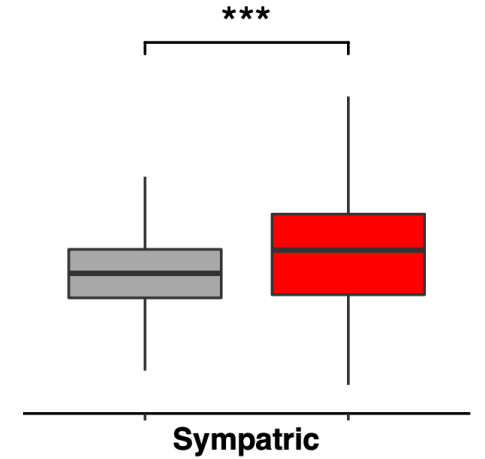
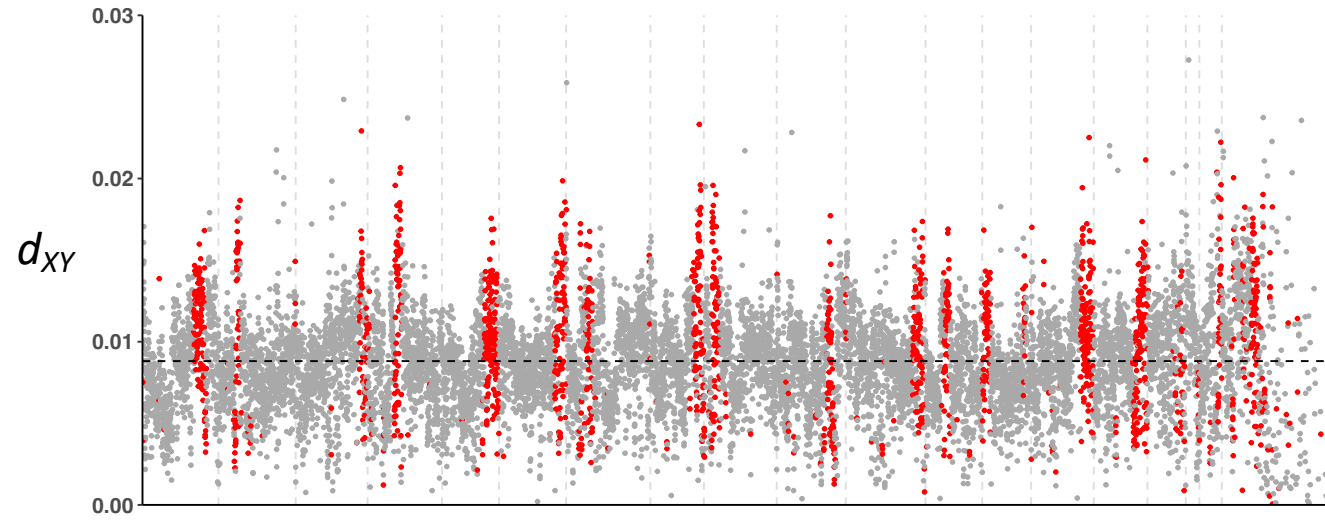
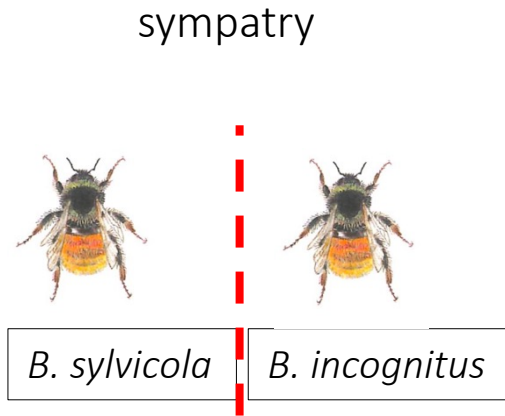


sympatry

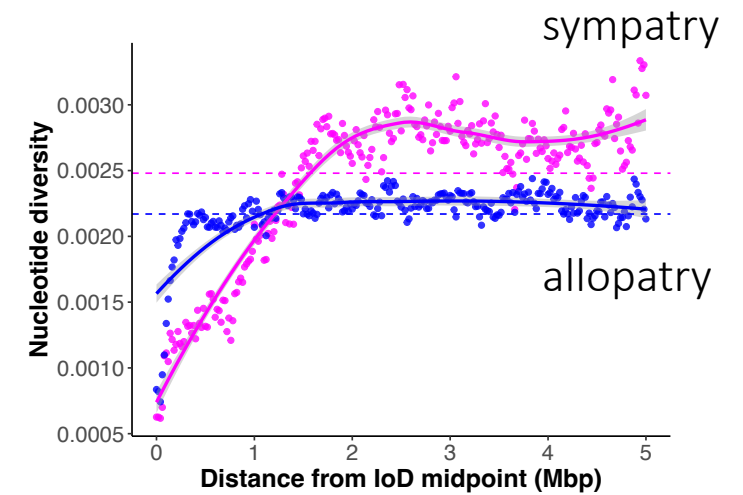
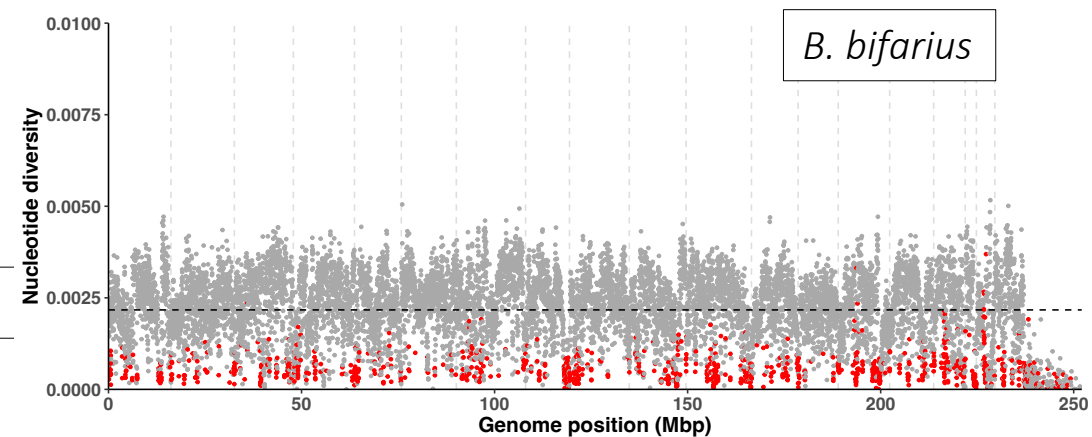
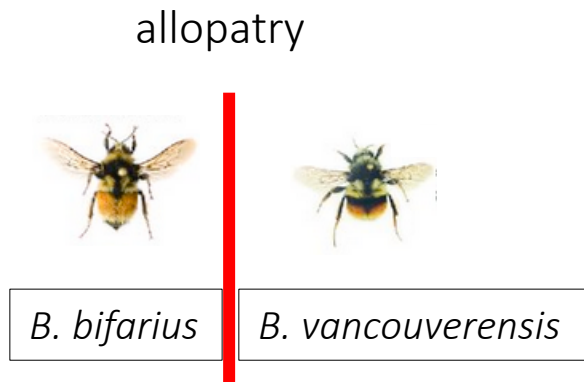
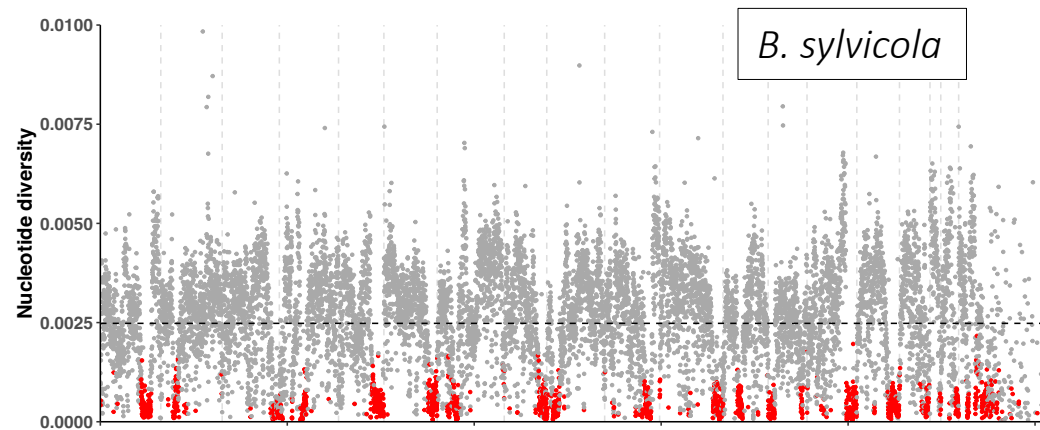
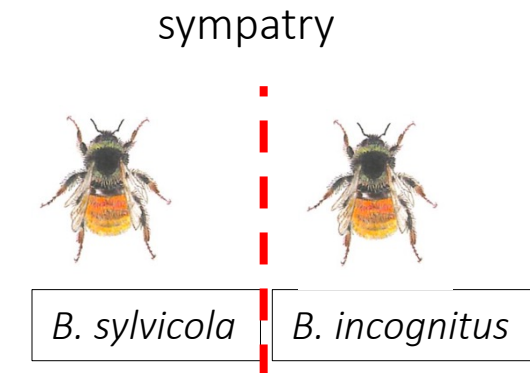


allopatry

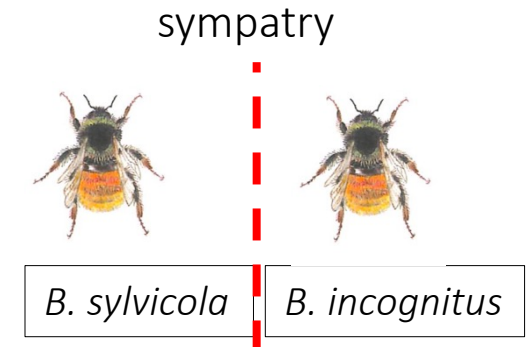
d_{XY} is elevated in islands of divergence in the sympatric, but not allopatric, comparison, indicating differential gene flow



Extensive reduction in nucleotide diversity around islands of divergence in sympatry

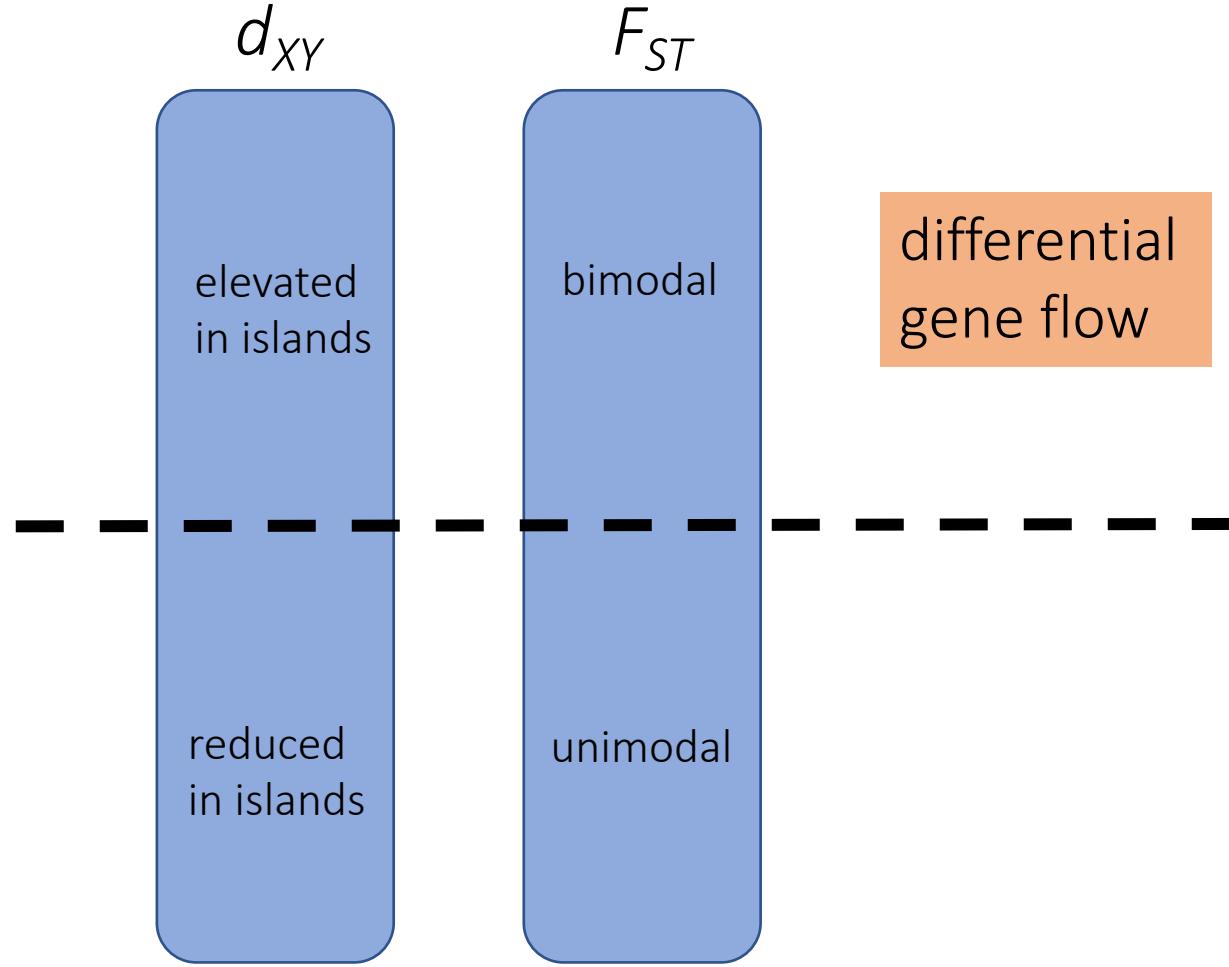
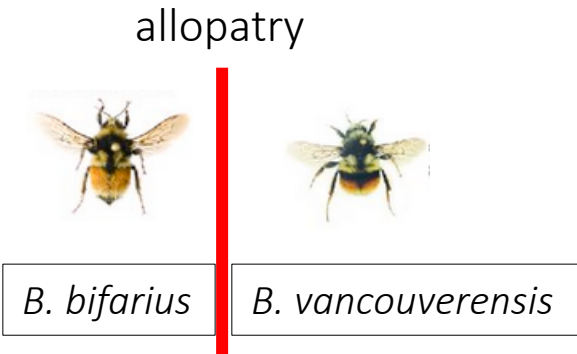


Genomic islands of divergence in sympatry and allopatry

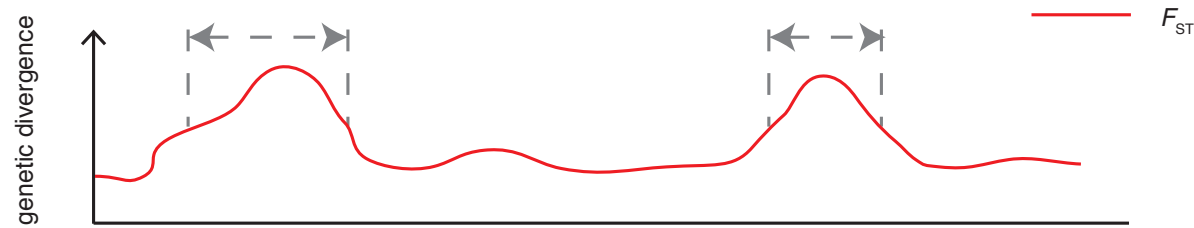


shared peaks of divergence
centromeres
reduced recombination

LINKED SELECTION

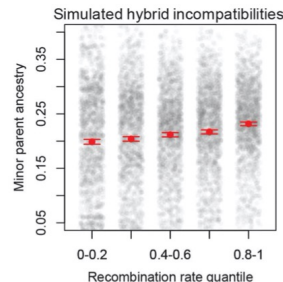


Genomic landscape of divergence

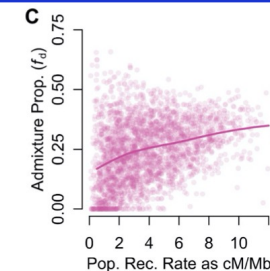
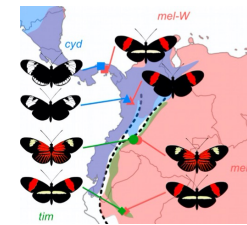


“Islands of speciation”
resistant to gene flow

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



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



Schumer *et al.* (2018) Science

Martin *et al.* (2019) PLoS Biol

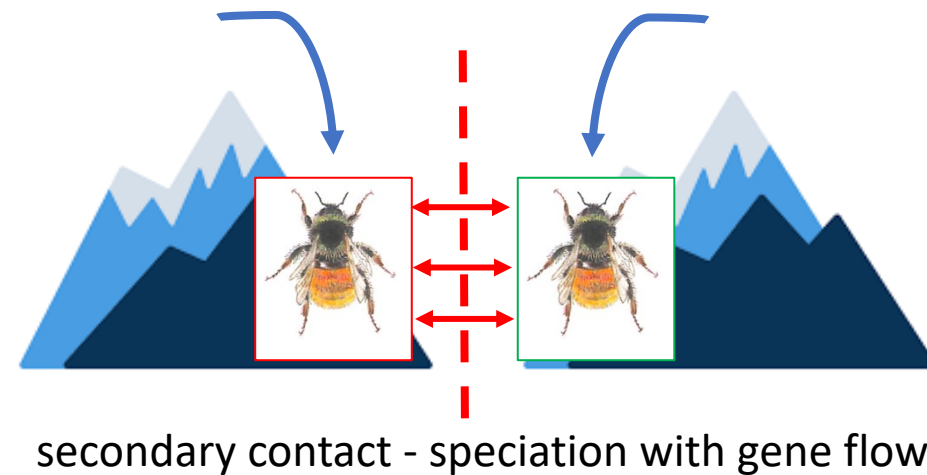
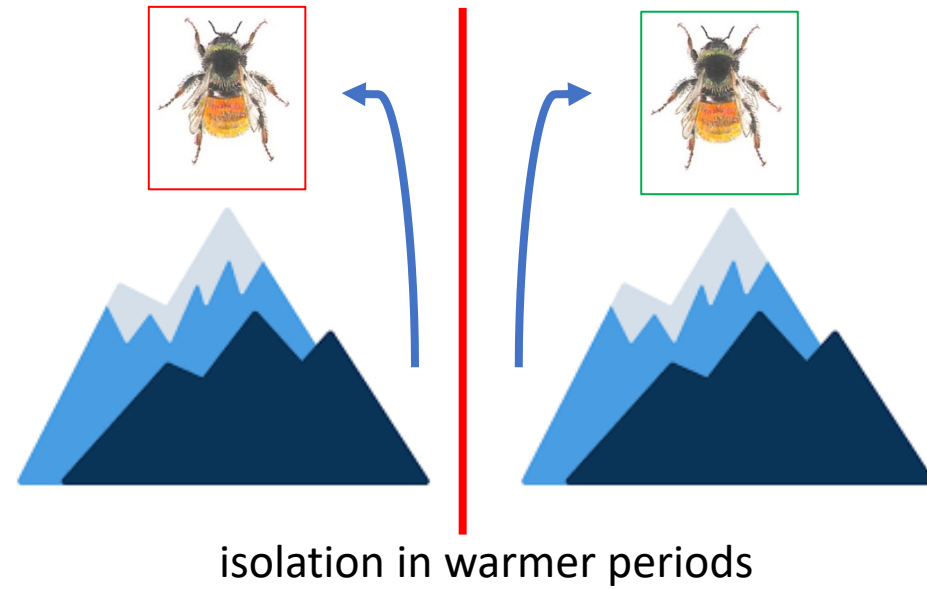
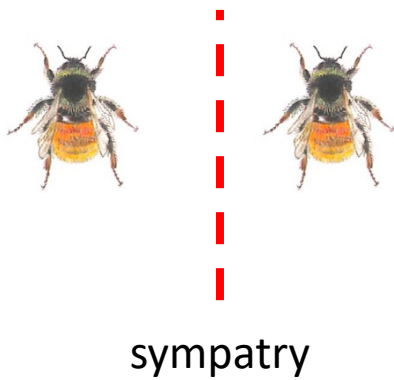
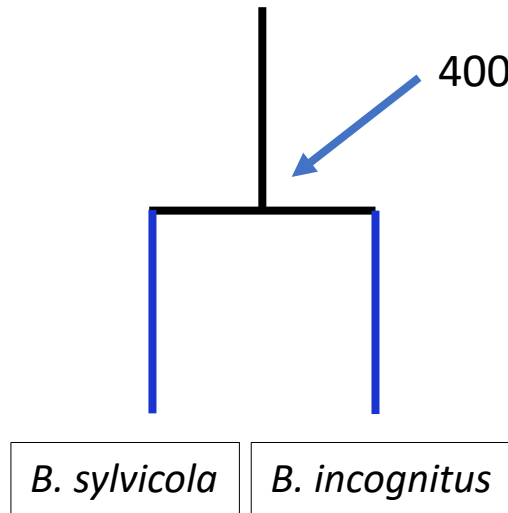
Summary: Speciation with gene flow



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

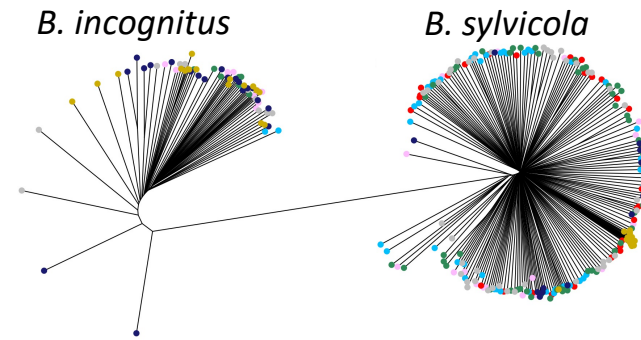
Genetics and body measurements reveal that four species of penguin have been masquerading as one...



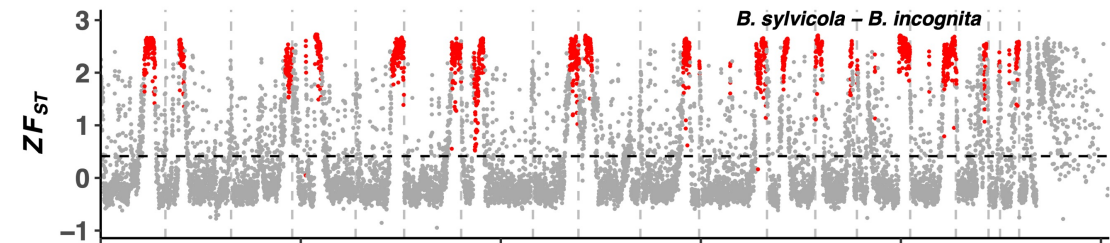
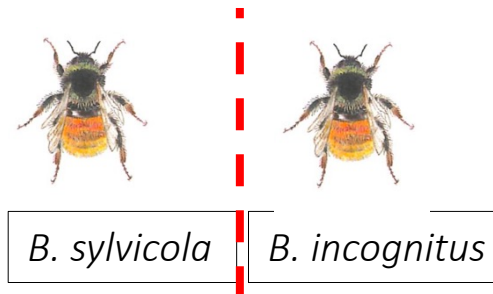
- How many more cryptic species?
- Is DNA evidence enough to define a new species?
- More resolution from genome sequencing compared to barcoding

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

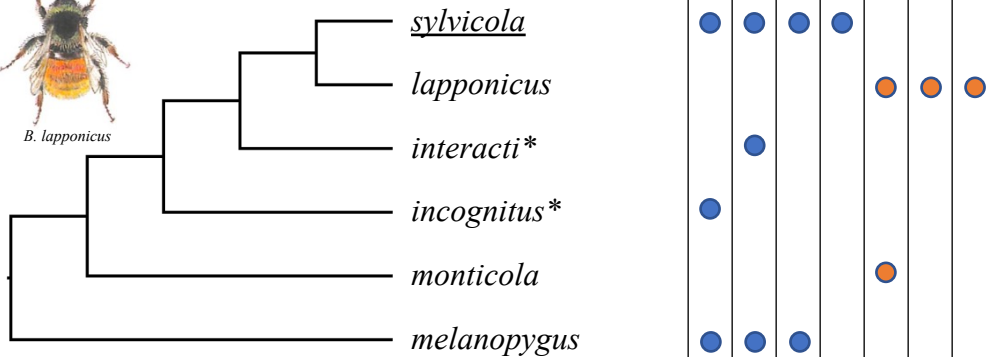


b)

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

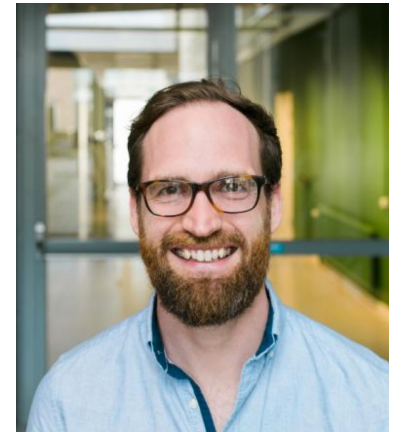
SciLifeLab / Uppsala University

Valentina Peona, Alexander Suh

Uppsala University / UEA, UK

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

Webster University / Appalachian State University, USA



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