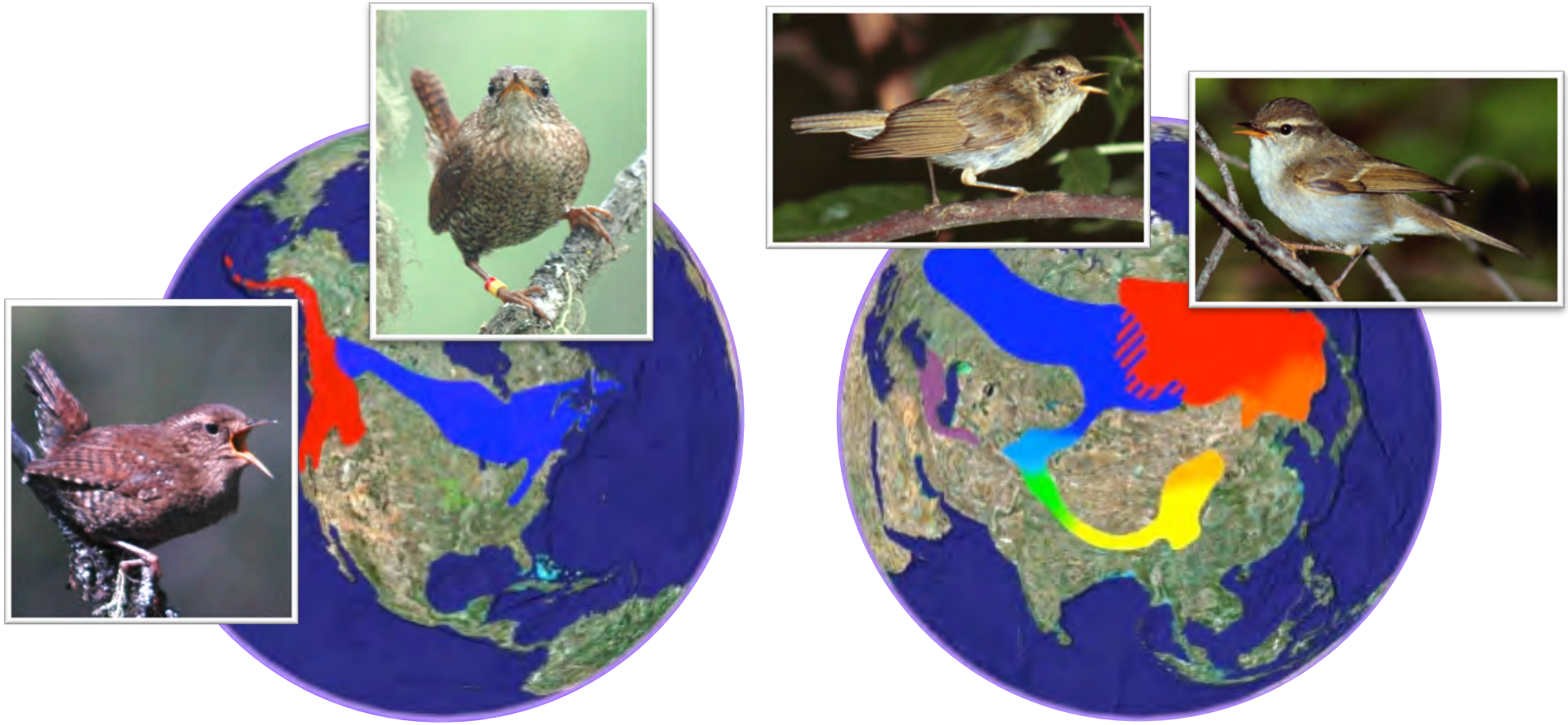
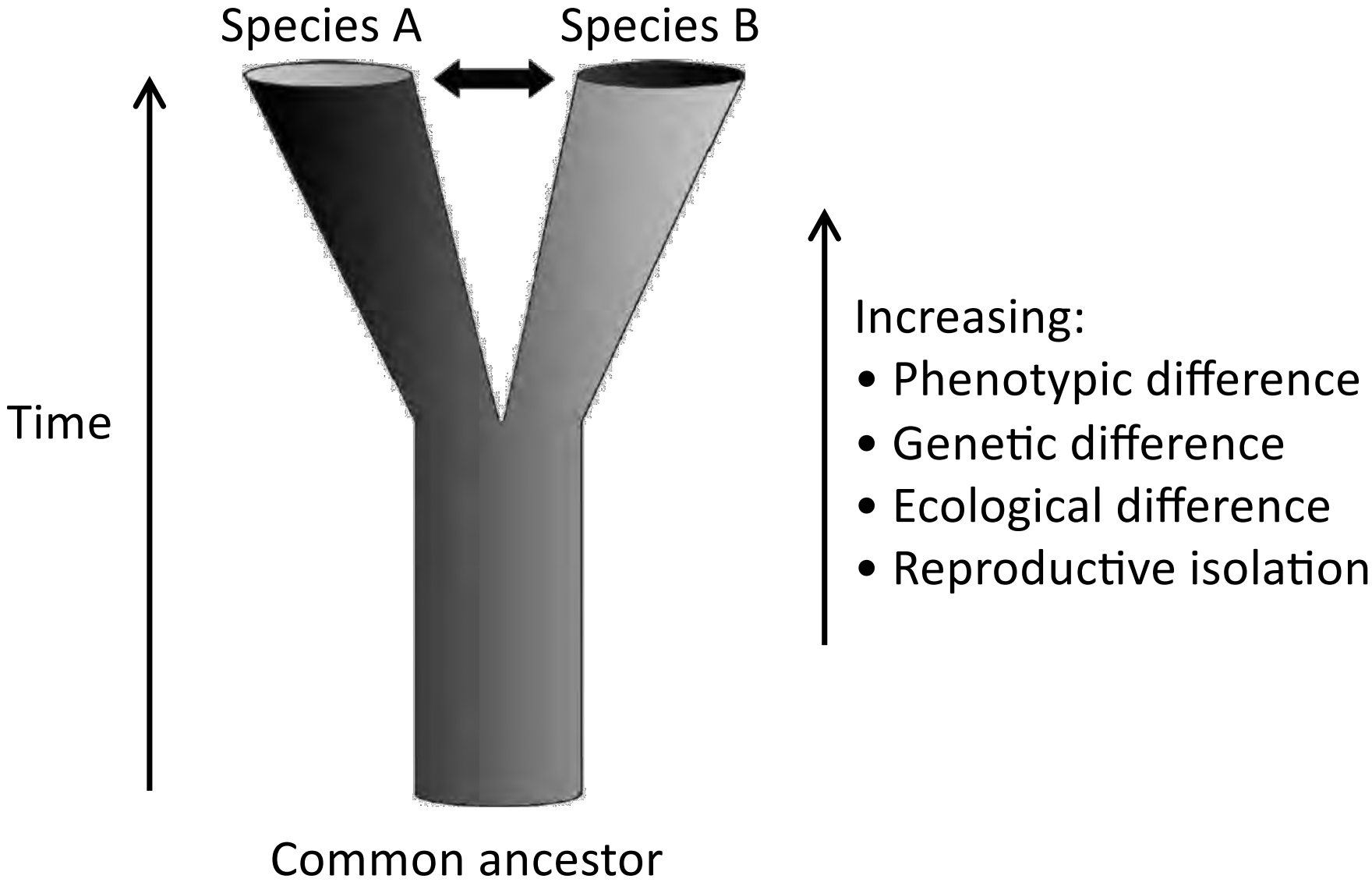
Geography and avian speciation



Darren Irwin

Zoogeography guest lecture, 23 Jan. 2019

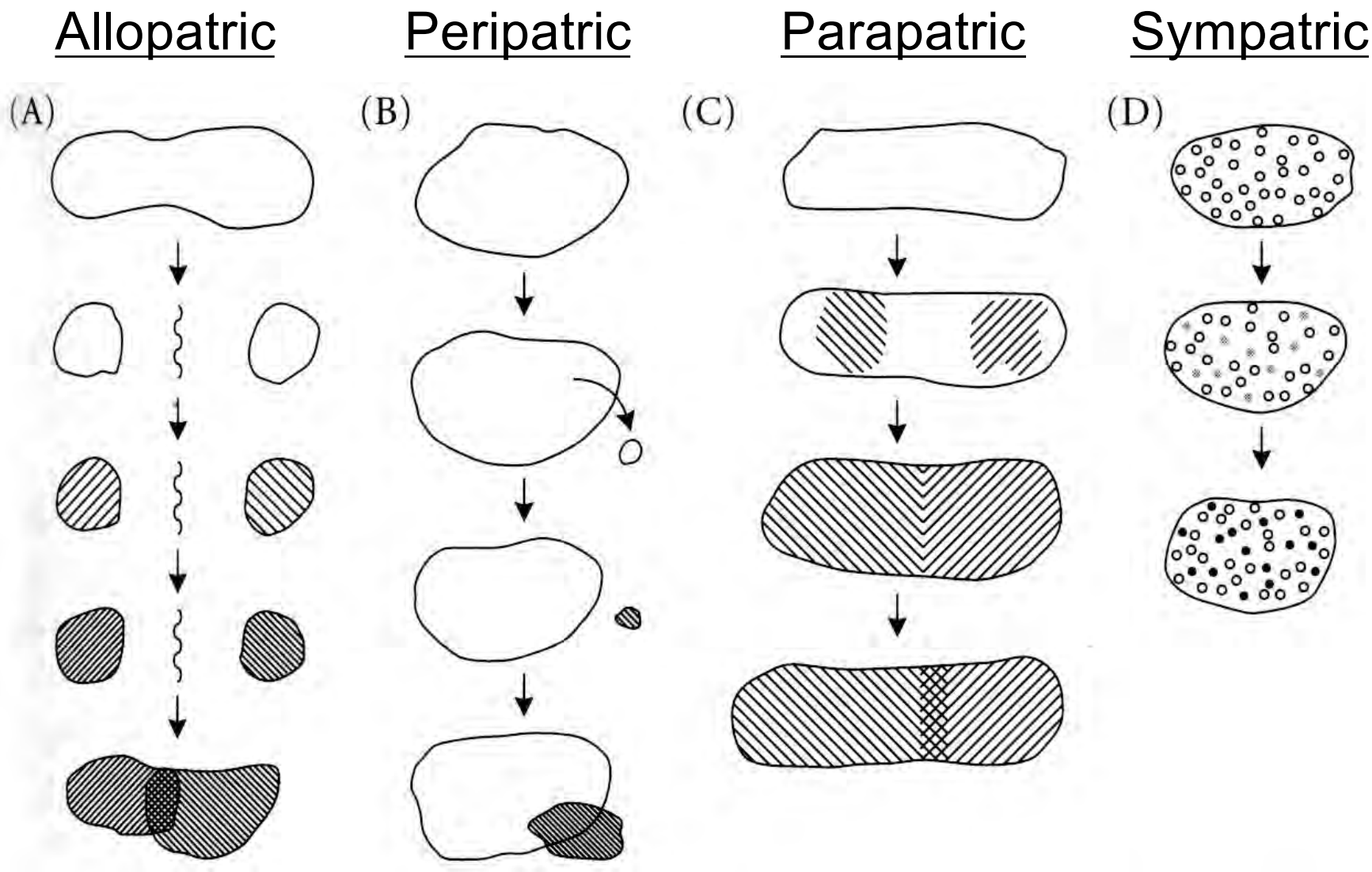
Speciation: the process by which one species evolves into two species.



Why care about speciation?

- Curiosity: A deep quest of humanity is to understand the origin of species.
- Conservation: To understand what is being lost, we need to understand patterns of biodiversity and the processes that produce it.
- Unexpected insights: Asking big questions often leads to surprising findings (e.g. about migration, adaptive introgression, etc.).

Four geographic models of speciation



Futuyma (1998) *Evolutionary Biology*. Sinauer.

In terrestrial vertebrates, allopatric speciation seems to be dominant

- **Jordan's Law:**
  - **"Given any species, in any region, the nearest related species is not to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort or at least by a belt of country, the breadth of which gives the effect of a barrier" (Jordan, 1908)**

Hybridization

Bob Steele

Bob Steele

Derrick Ditchburn

http://www.bobsteelephoto.com

http://www.dereila.ca

Big questions regarding speciation

- What is the typical time course of speciation?
- How important are geographic barriers?
- Does hybridization play an important role?
- What processes generate reproductive isolation?
  - Drift? Natural selection? Sexual selection?
- What is a species?

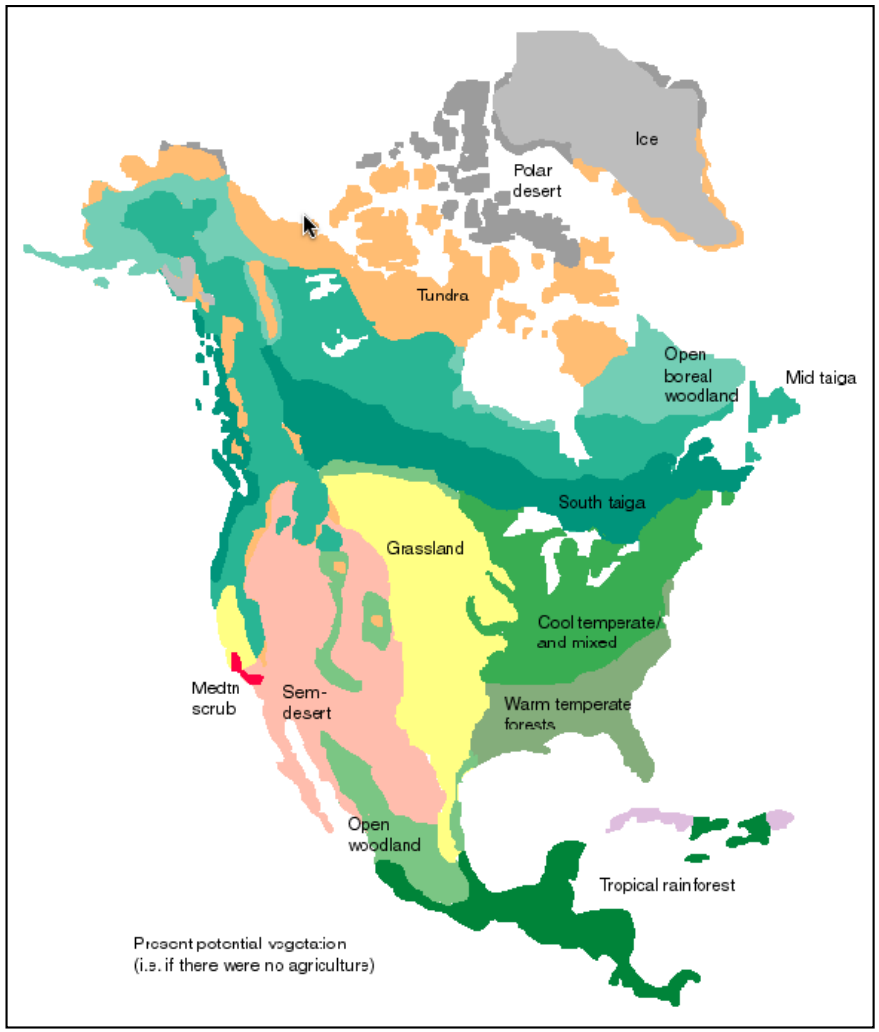
Evolving views of the role of hybridization in speciation

- Hybridization has usually been viewed as evidence of blending of forms, working against speciation.
  - mid-1900's "reign of terror" of the Biological Species Concept led to many species being lumped.
- In 1980's-1990's, idea of stable hybrid zones developed, with selection against hybrids balanced by gene flow into the zone. ("tension zone"; e.g. Barton)
  - Part of the genome flows between species, but part does not (e.g. Wu's "genic view of speciation").
- More recently: Source of adaptive introgression, fostering further evolution of each form? (e.g. Rieseberg)

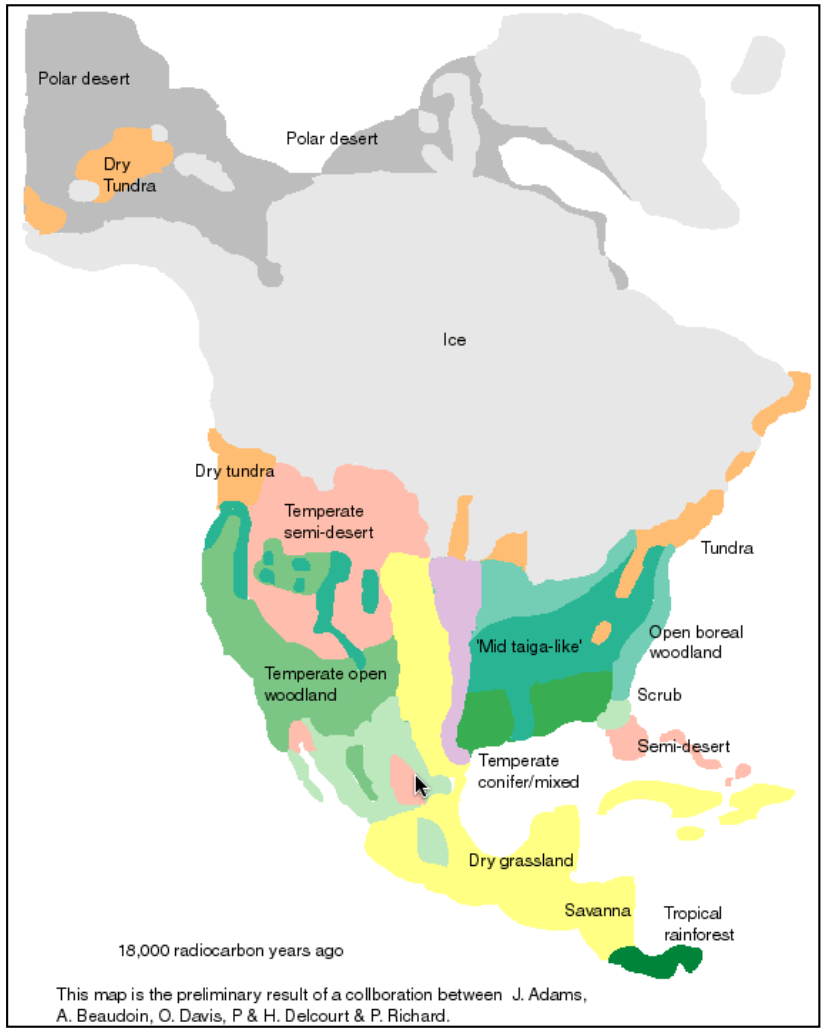
Plan for the talk

I. Overview of patterns in the Great Canadian Suture Zone.
II. A close look at the role of seasonal migration in speciation, as well as its genetic basis.
III. Biogeography of the Greenish Warbler ring species.

North America, now and then

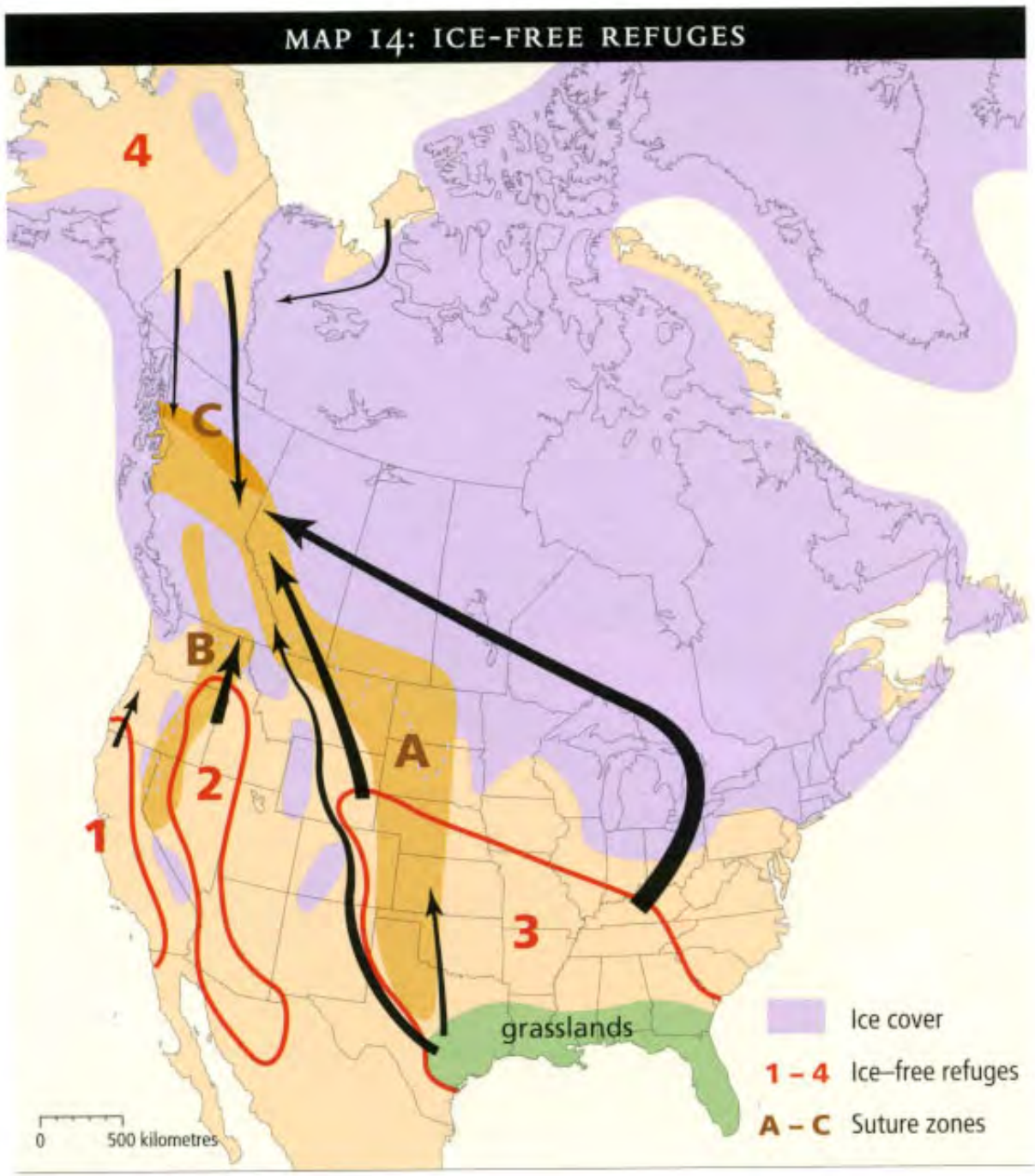


now

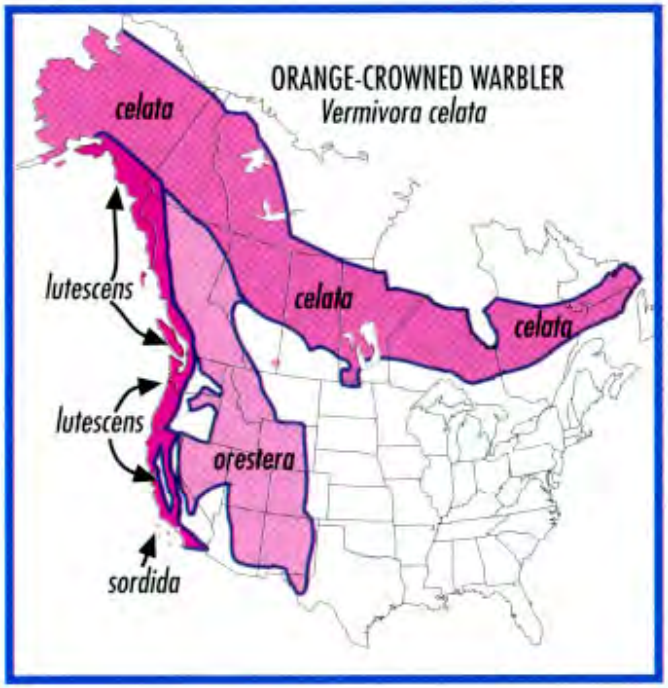


~18,000 years ago

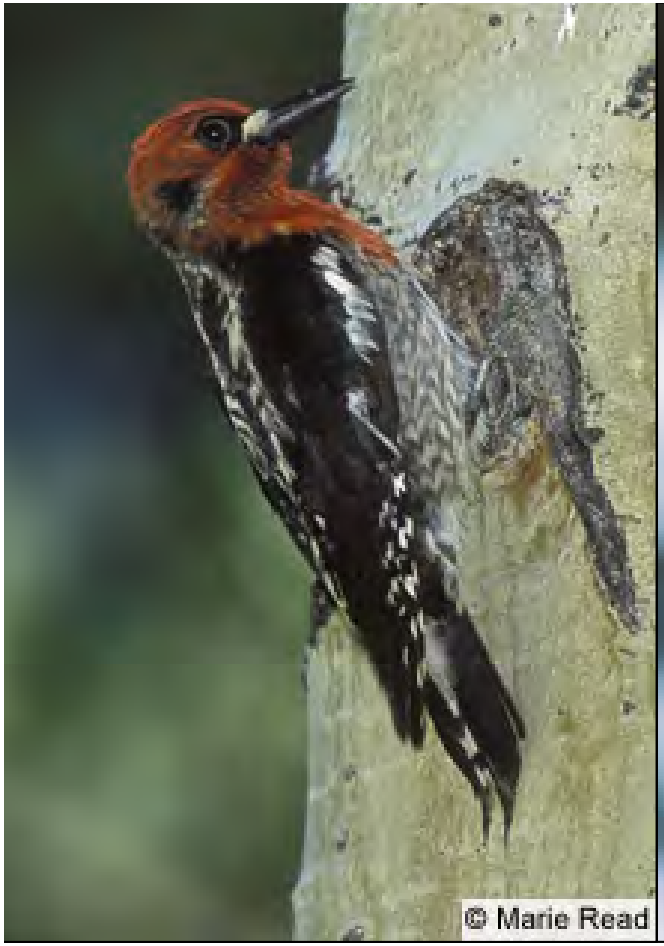
Source: Quaternary Environments Network (http://www.esd.ornl.gov/projects/qen/nerc.html)



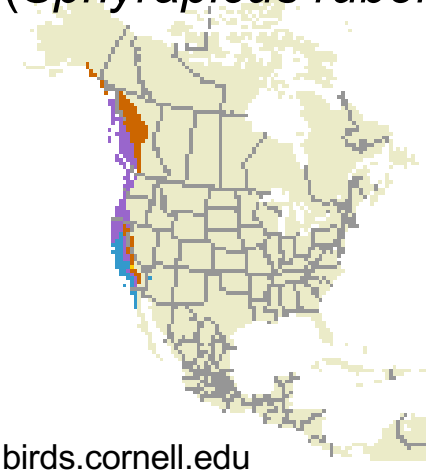
Suture Zones: places where divergent biota meet



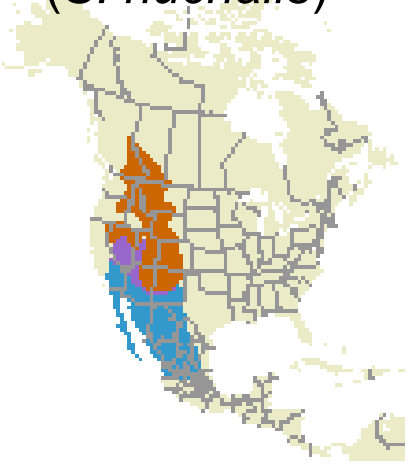
Cannings & Cannings (2004) *British Columbia: A Natural History*. Greystone Books, Vancouver.



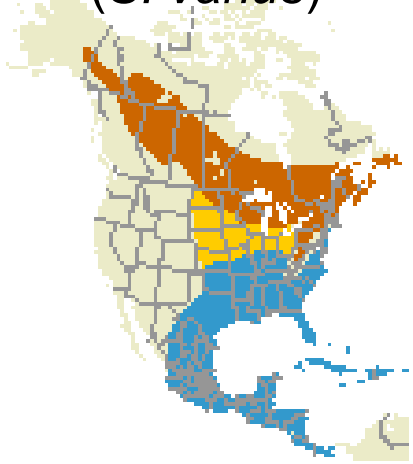
Red-breasted Sapsucker
(*Sphyrapicus ruber*)



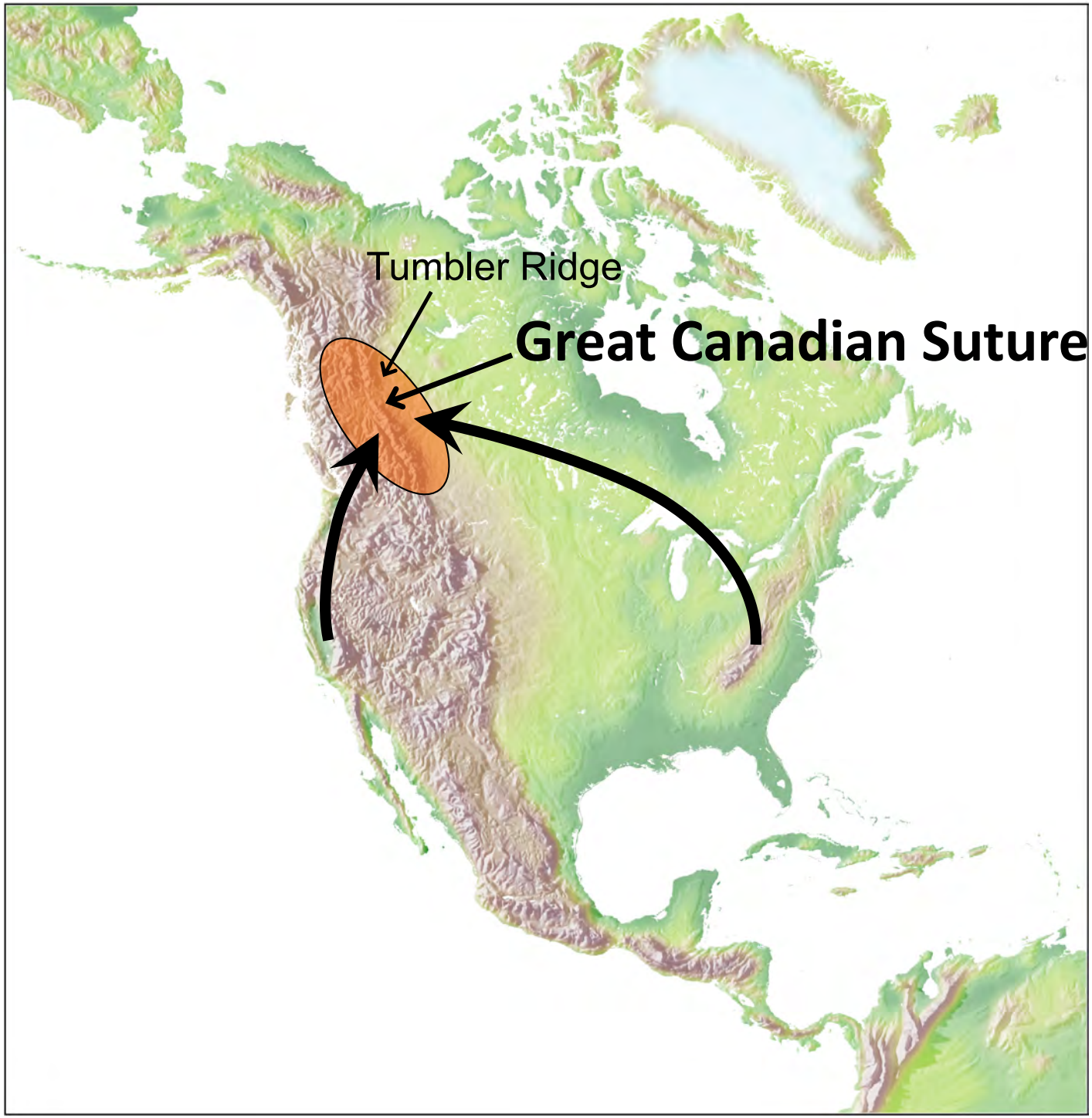
Red-naped Sapsucker
(*S. nuchalis*)



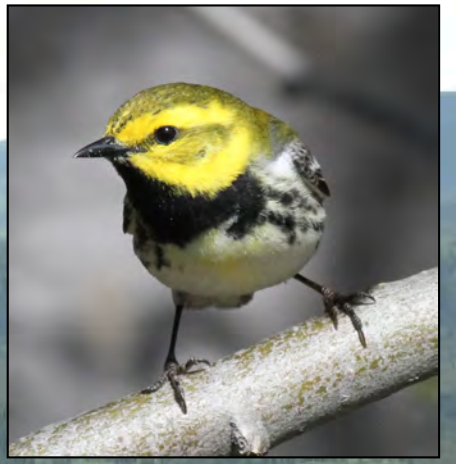
Yellow-bellied Sapsucker
(*S. varius*)

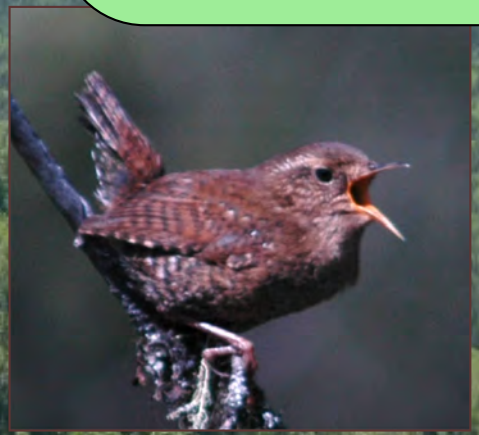


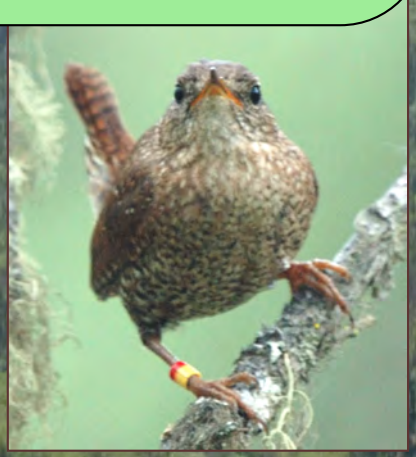
www.birds.cornell.edu


Tumbler Ridge
Great Canadian Suture Zone

Genes (mtDNA and nDNA)
Songs and calls (response too)
Body shape, size, and color
Habitat and ecology
Seasonal migratory behavior

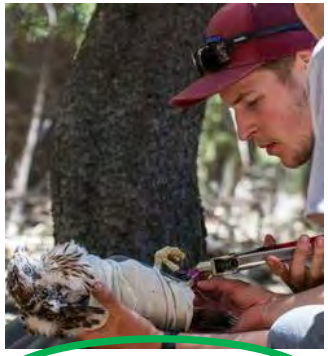






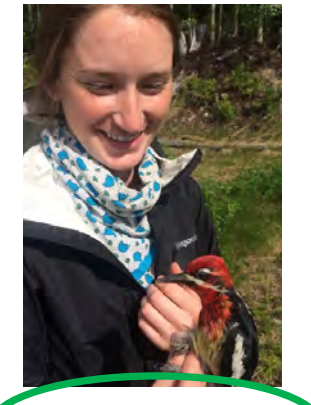
The Team

Dr. Sampath Seneviratne



Kenny Askelson

Silu Wang



Libby Natola

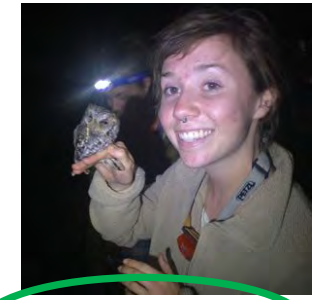
Dr. Armando Geraldes

Annegret Liederbach

Dr. Julie Lee-Yaw

Dr. David Toews

Rashika Ranasinghe



Madelyn Ore

Ellen Nikelski

Else Mikkelsen

Dr. Christine Grossen

Dr. Miguel Alcaide

Dr. Kira Delmore

Alison Porter

Haley Kenyon

Jessica Irwin

Dr. Alan Brelsford

Surprising finds from the contact zone

One species that is really two species:

Pacific / Winter Wrens

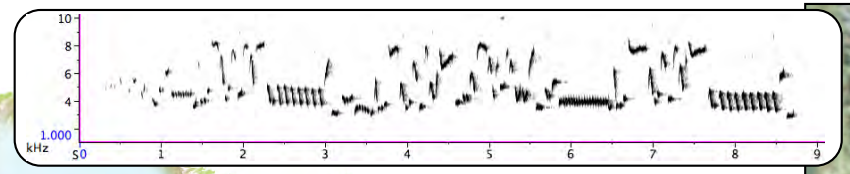
Distinct species that hybridize extensively:

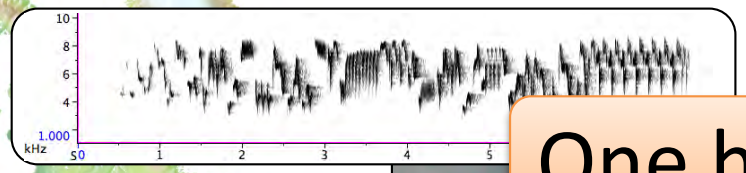
Townsend's / Black-throated Green Warblers

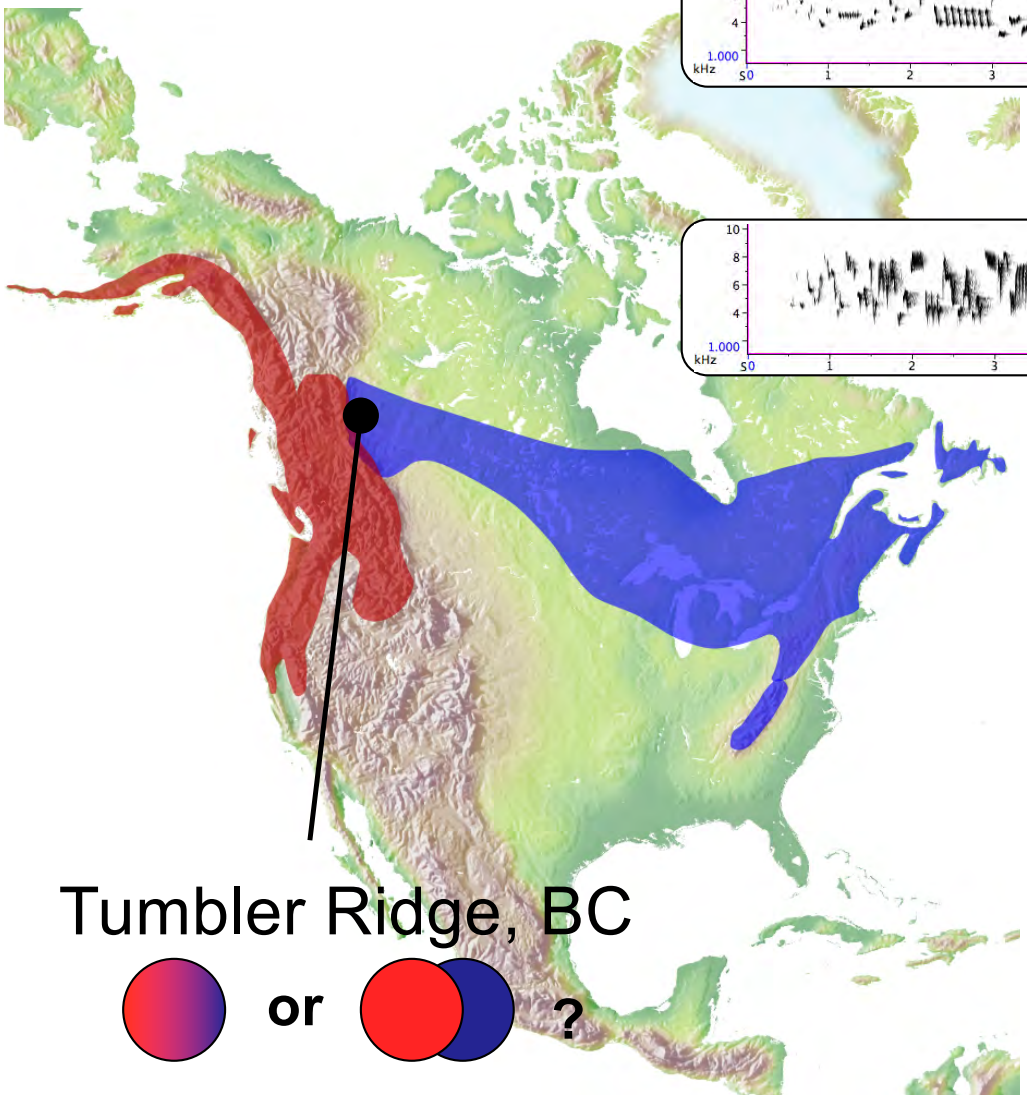
MacGillivray's / Mourning Warblers

Pacific / Winter Wrens (*Troglodytes pacificus / hiemalis*)

- Treated as single species until 2010.
- Were then split into two species based on our finding of distinct groups living in sympatry (Toews & Irwin 2008). Genetic divergence time roughly 4.3 MYA!

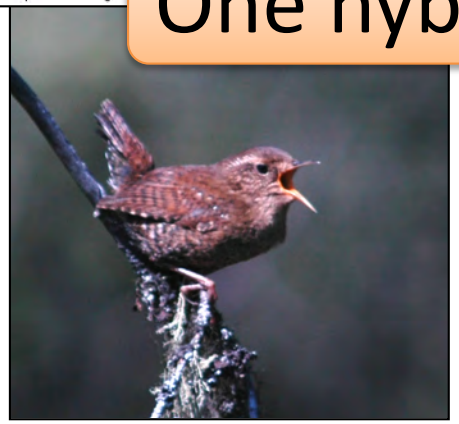




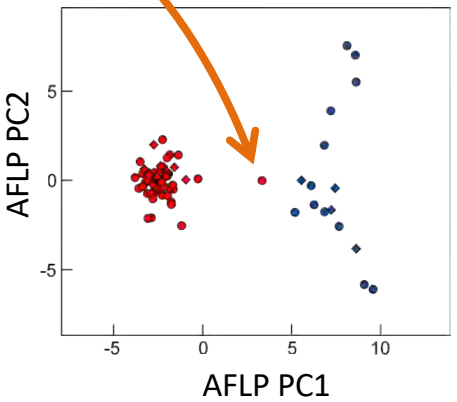


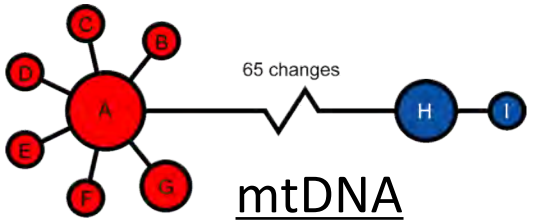
Tumbler Ridge, BC

One hybrid!



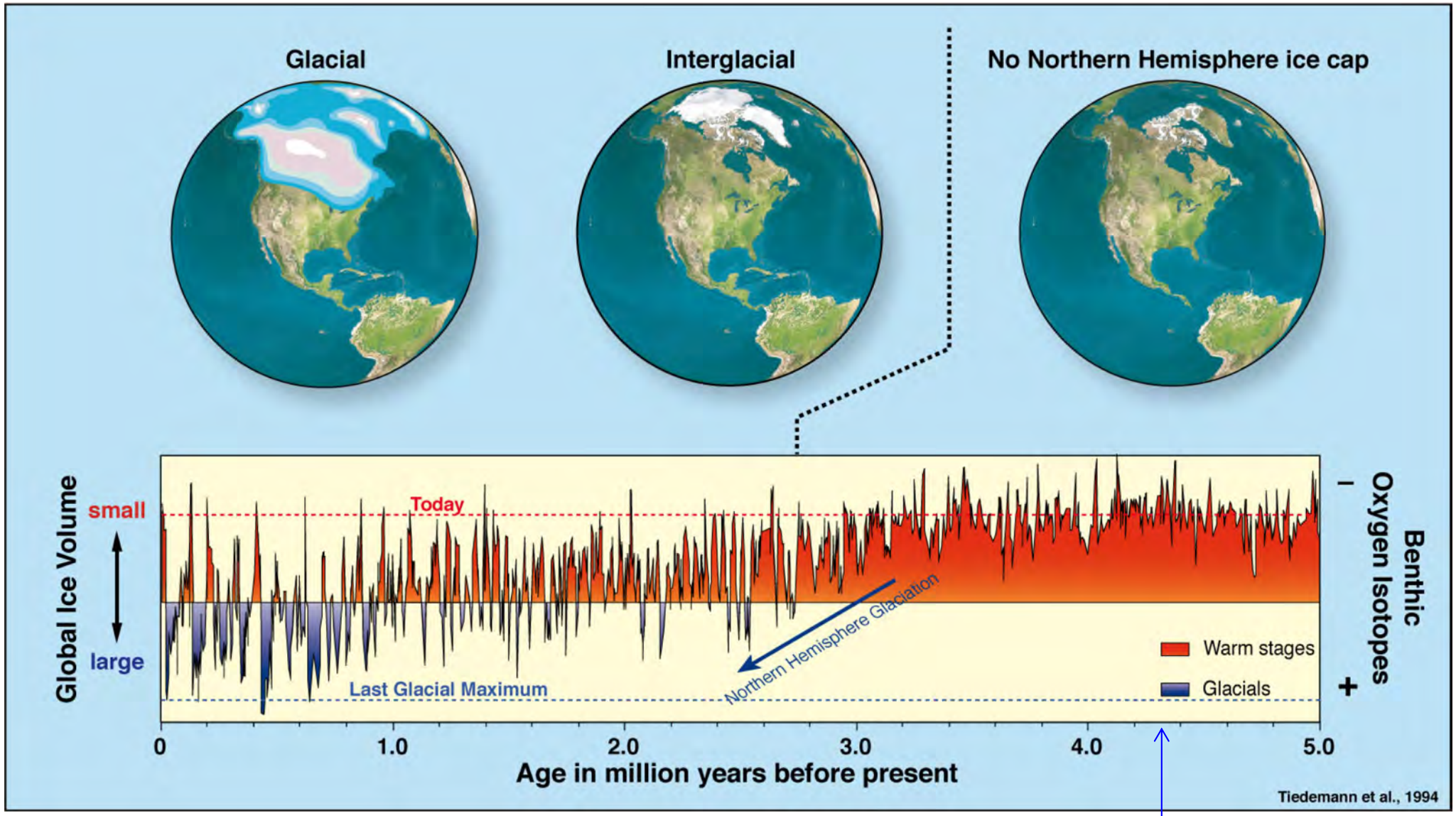
nDNA





mtDNA

Photos: D. Irwin



Pacific wren

Winter wren

Wrens have experienced many glacial cycles!

Surprising finds from the contact zone

One species that is really two species:

Pacific / Winter Wrens

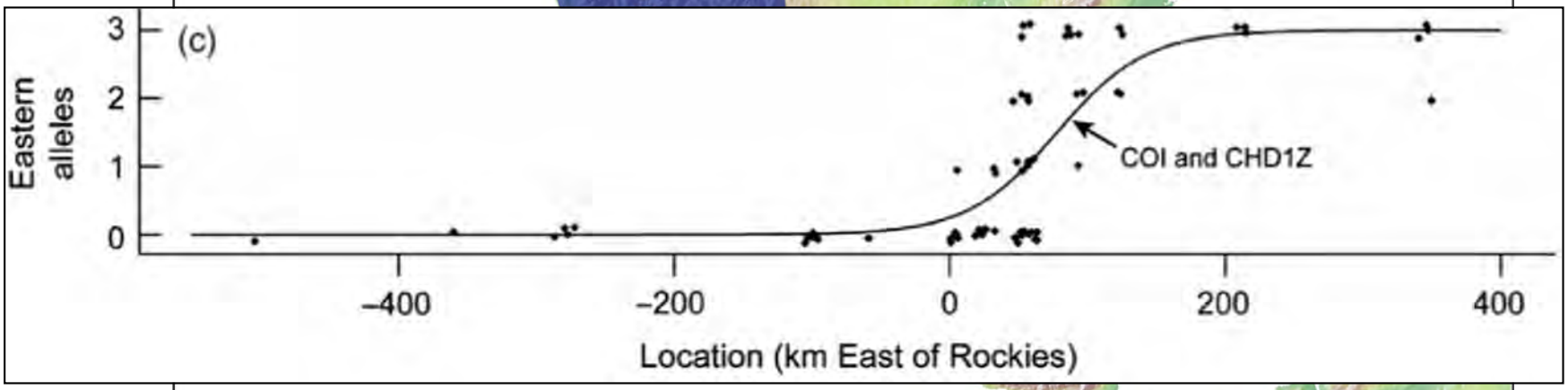
Distinct species that hybridize extensively:

Townsend's / Black-throated Green Warblers

MacGillivray's / Mourning Warblers

Narrow hybrid zone

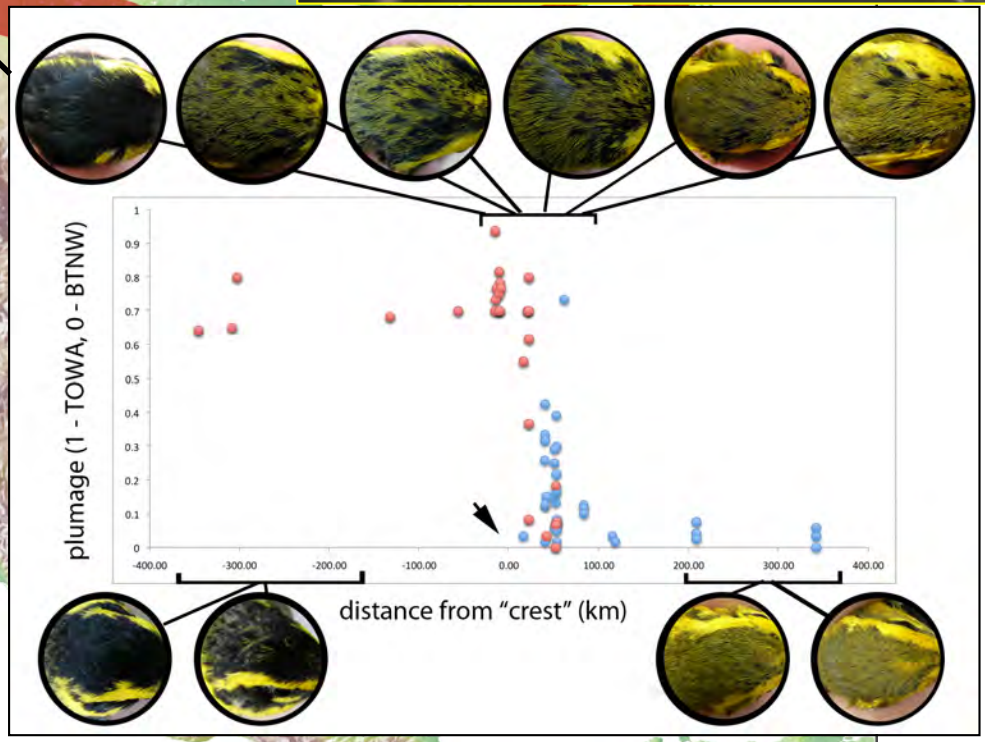
(Irwin et al. 2009)



MacGillivray's / Mourning Warblers
(*Oporornis tolmiei* / *O. philadelphia*)

Narrow hybrid zone

(Toews, Brelsford, & Irwin 2011)



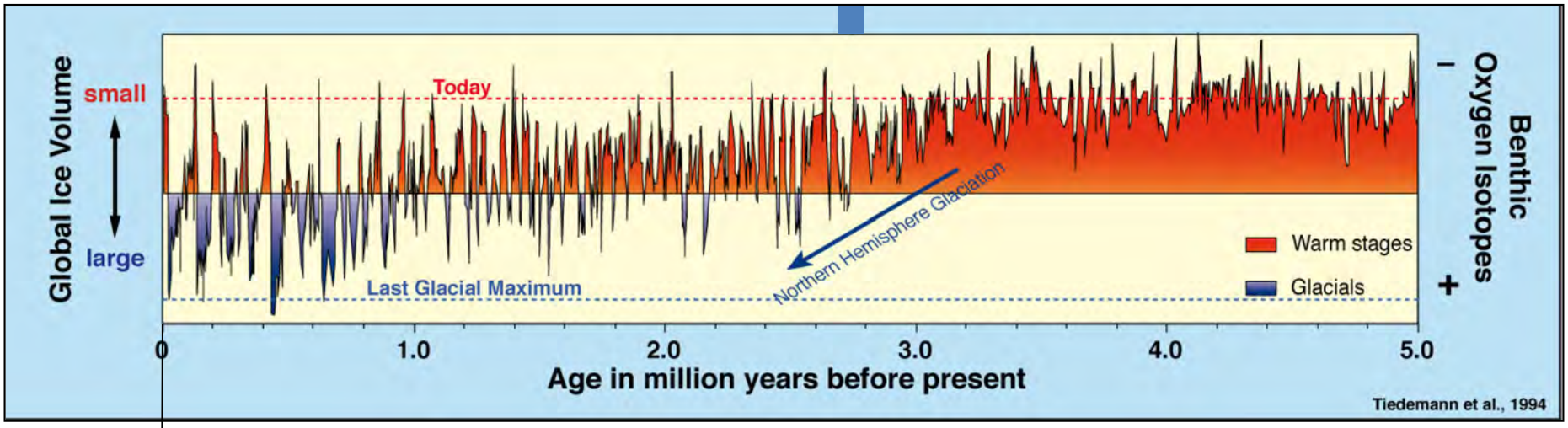
Townsend's / Black-throated Green Warblers

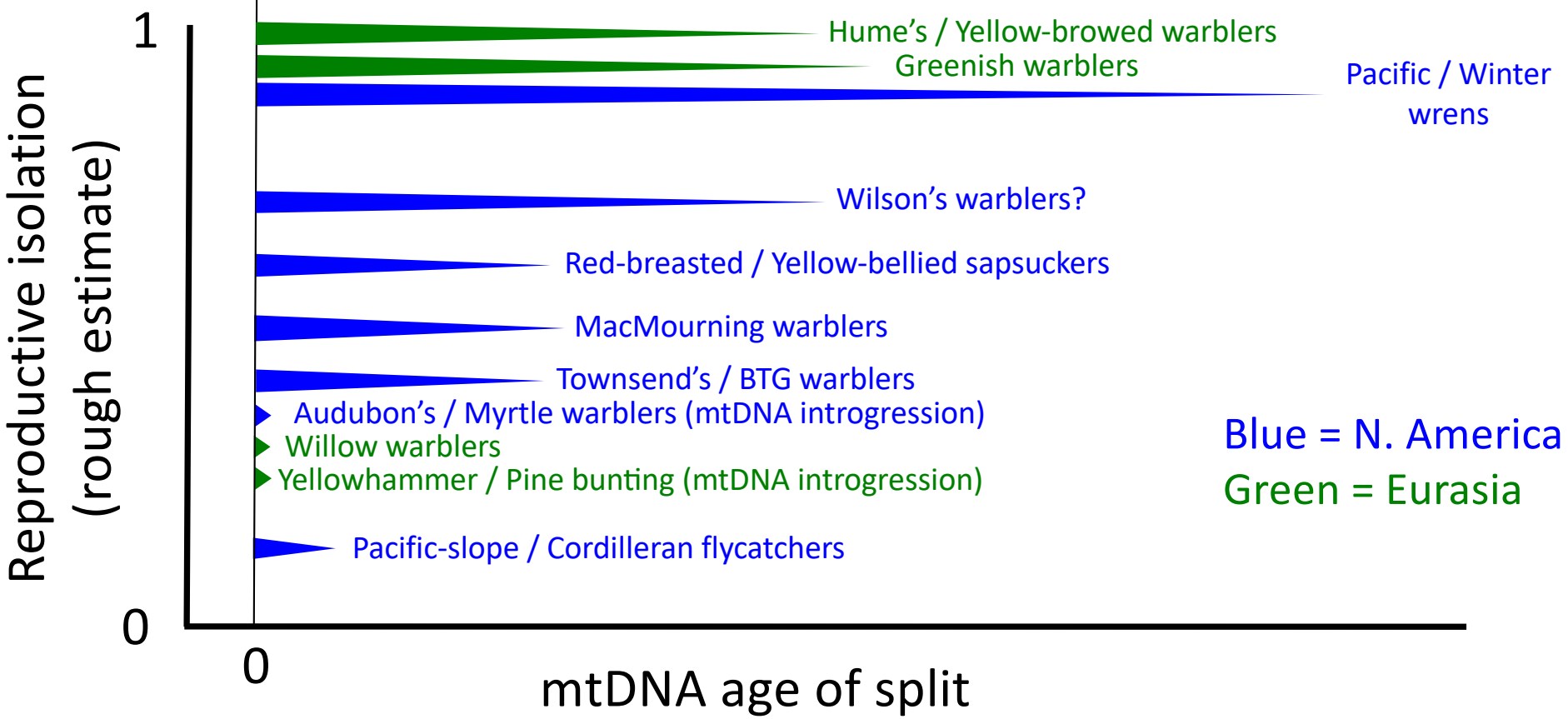
(*Dendroica townsendi* / *D. virens*)

Lessons from narrow hybrid zones:

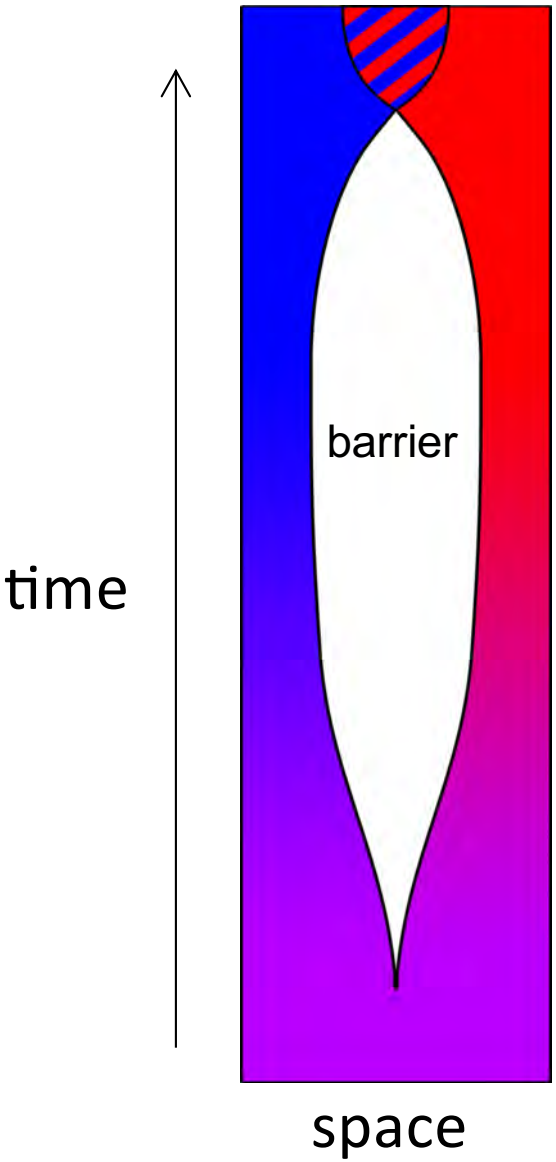
- Taxa treated as distinct species are often found to hybridize extensively.
- Narrow zone suggests selection.
  - Much of genome can flow across hybrid zone, but parts under divergent selection are stopped (see work by Barton, Wu, and others).
  - “Tension Zone” model: reduced fitness of hybrids balanced by net gene flow into the zone.

Putting all the case studies together . . .


Global Ice Volume
small
large
Today
Last Glacial Maximum
Northern Hemisphere Glaciation
Warm stages
Glacials
Benthic Oxygen Isotopes
–
+
0
1.0
2.0
3.0
4.0
5.0
Age in million years before present
Tiedemann et al., 1994

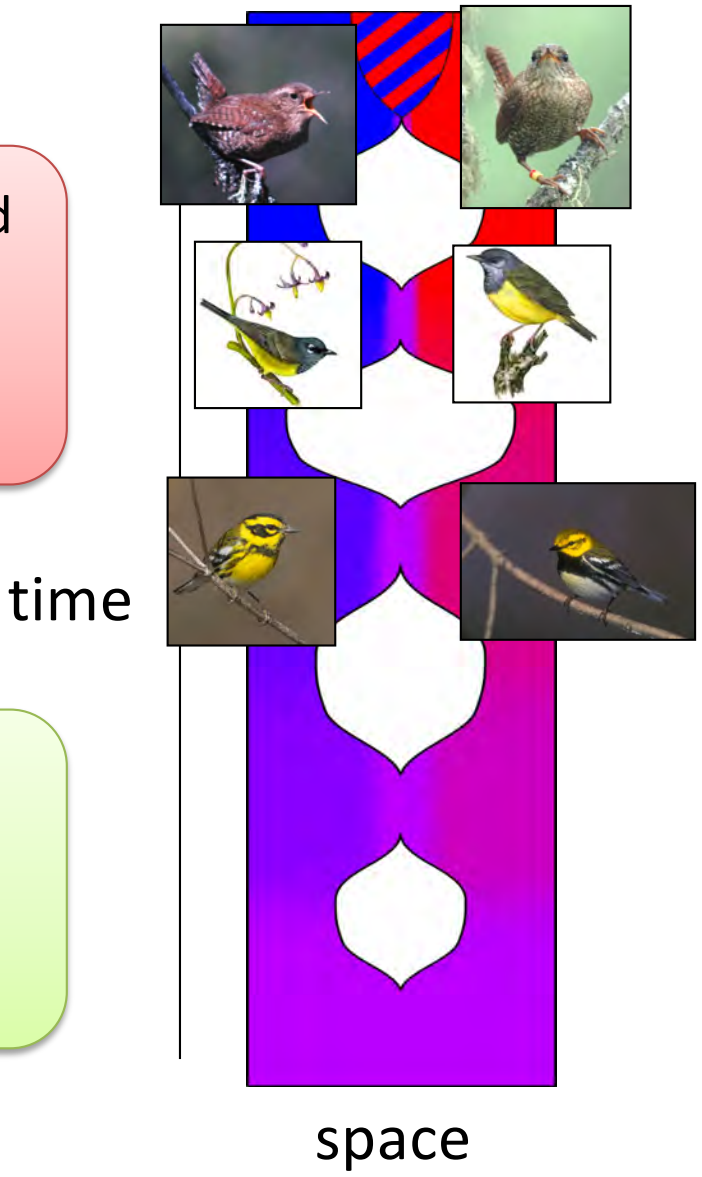

Reproductive isolation (rough estimate)
1
0
0
mtDNA age of split
Hume's / Yellow-browed warblers
Greenish warblers
Pacific / Winter wrens
Wilson's warblers?
Red-breasted / Yellow-bellied sapsuckers
MacMourning warblers
Townsend's / BTG warblers
Audubon's / Myrtle warblers (mtDNA introgression)
Willow warblers
Yellowhammer / Pine bunting (mtDNA introgression)
Pacific-slope / Cordilleran flycatchers
Blue = N. America
Green = Eurasia

Allopatric vs. cyclic isolation-hybridization speciation



Traditionally, hybrid zones have been viewed as working against speciation.

In these cases, speciation appears to proceed despite hybridization.



What could cause reduced gene flow across a hybrid zone?

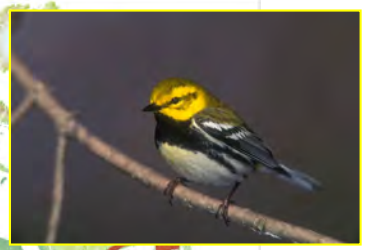
- Assortative mating (i.e., premating isolation).

In these cases, little evidence for much assortative mating early in speciation.

- Low fitness of hybrids (i.e., postmating isolation).
  - Intrinsic incompatibilities? Migratory behavior?

Pacific / Winter Wrens

Toews & Irwin 2008



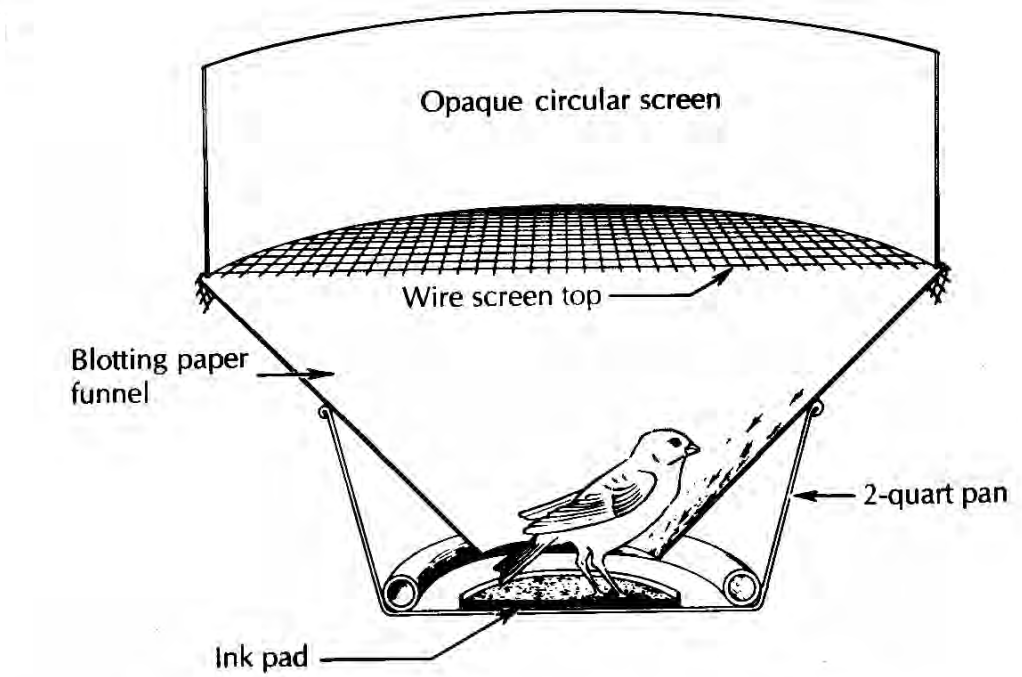
MacGillivray's / Mourning Warblers

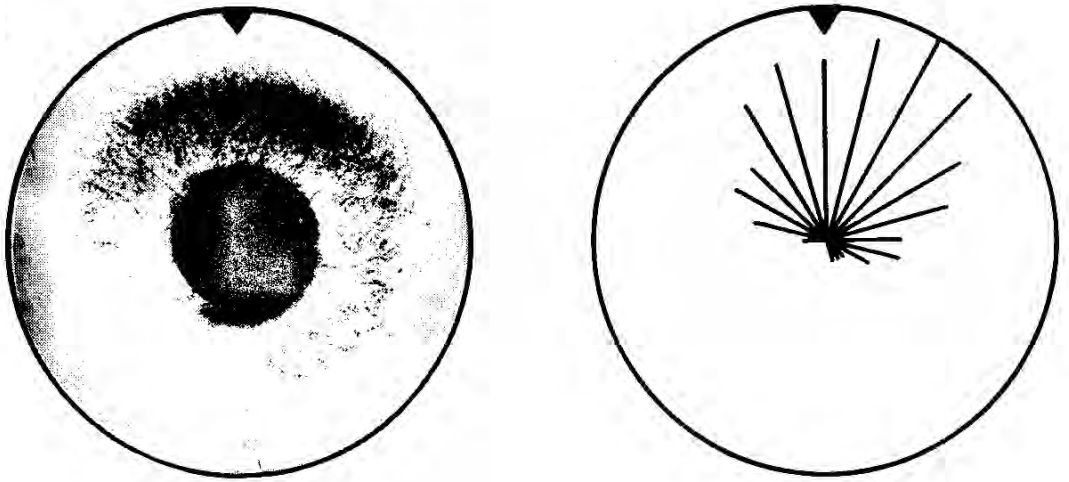
Townsend's / B-T Green Warblers

Emlen cages

Captive birds often display migratory restlessness, jump in preferred direction

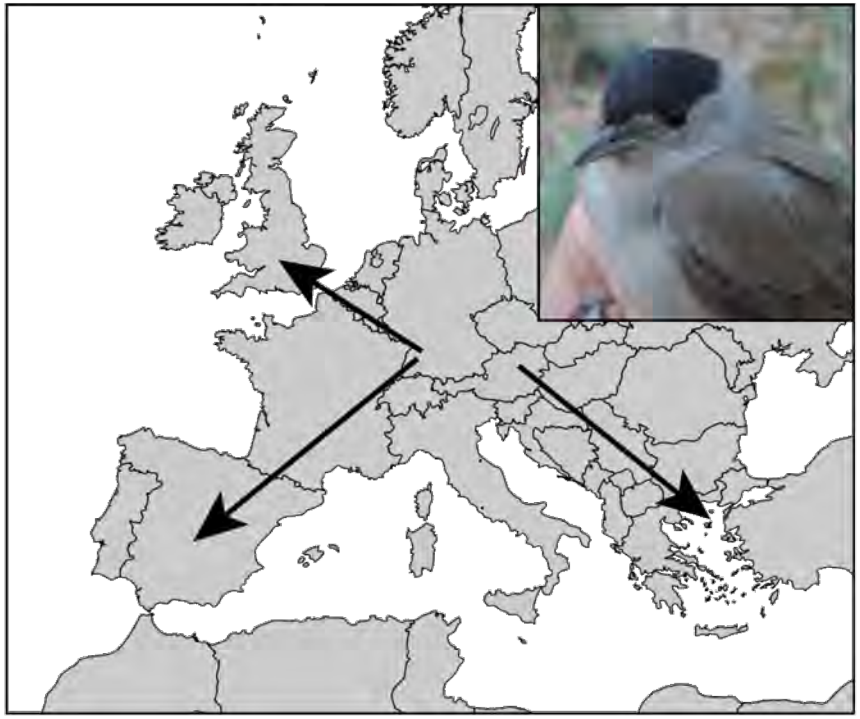
Most songbirds migrate alone, at night, with parents leaving before offspring.





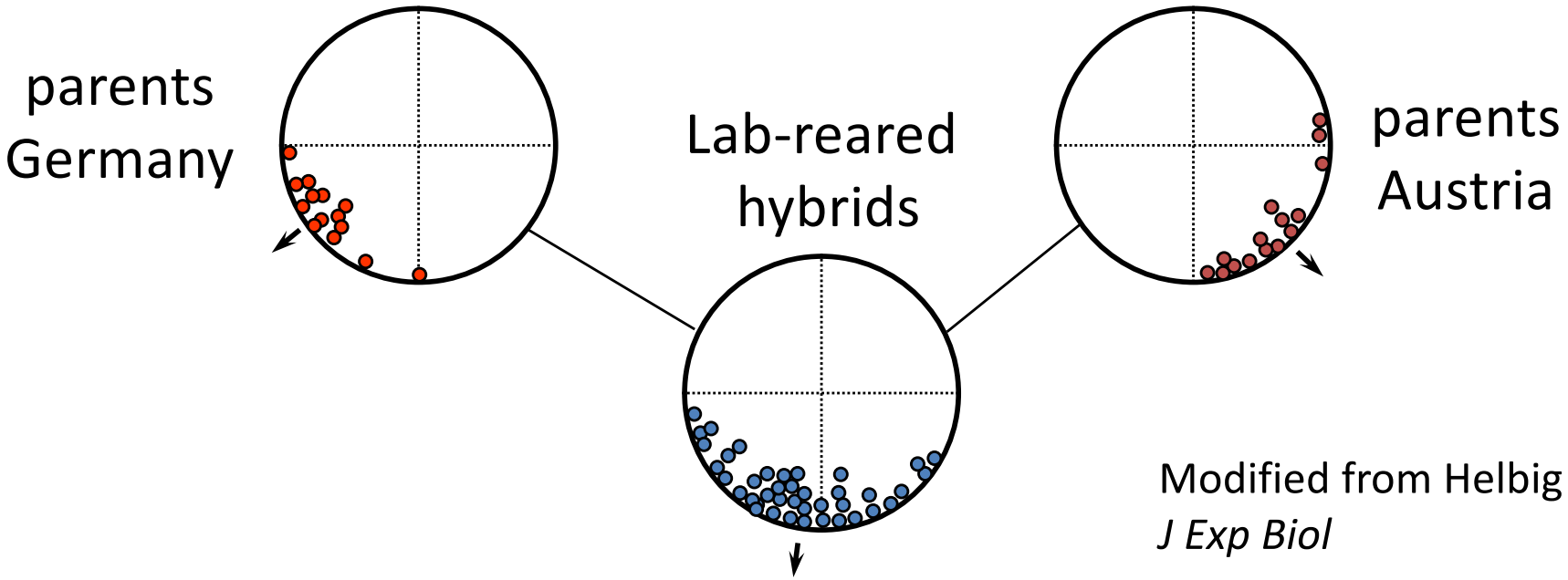
Emlen 1966

Helbig's studies showing genetic inheritance of migratory direction:
Blackcap warblers in Europe



Irwin 2009, Current Biology

Instinctive orientation in Fall:



Modified from Helbig 1996
J Exp Biol

Examples of “Migratory Divides”

Might hybrids have inferior routes?

Part II:

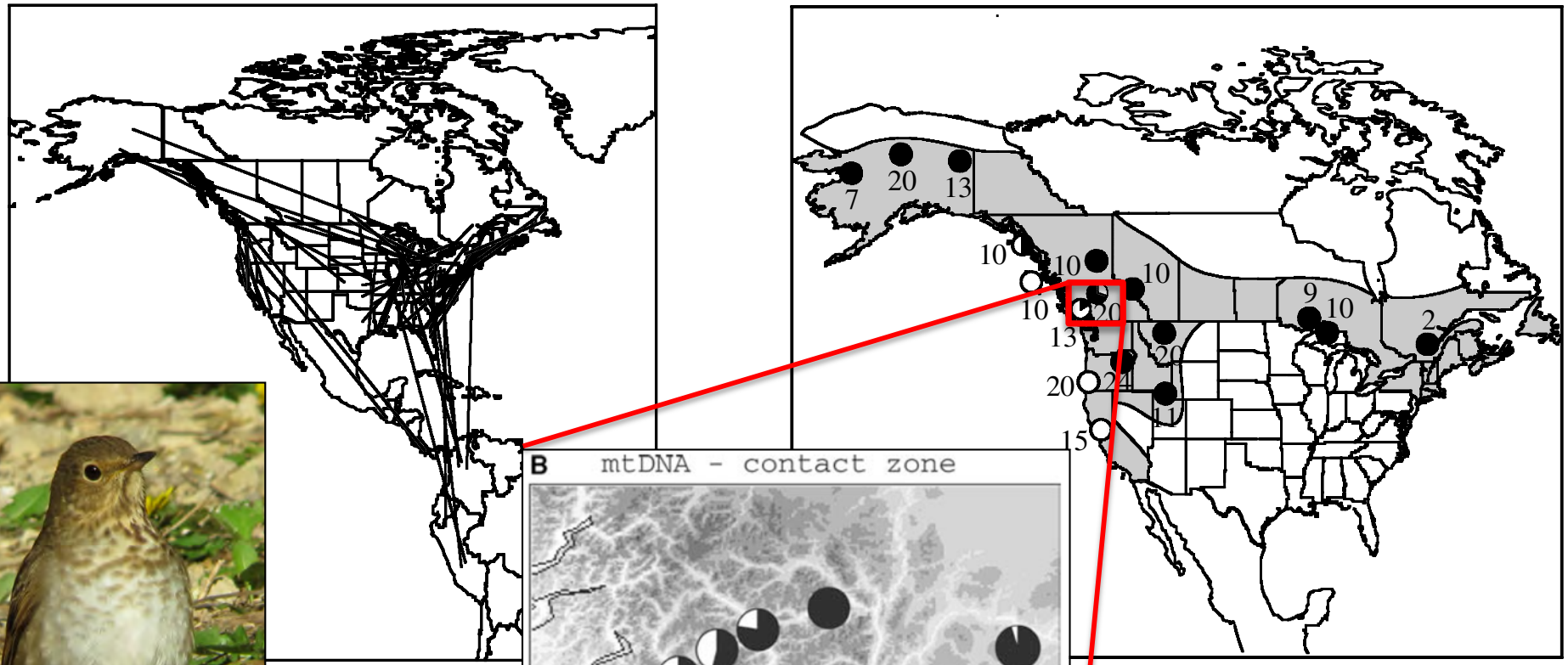
Testing the migratory divide hypothesis in wild, free-flying birds.

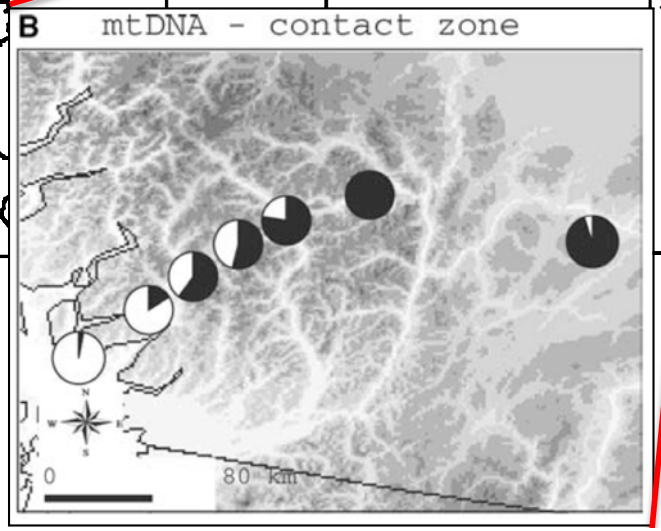
Dr. Kira Delmore

The study system: a hybrid zone between western and eastern forms of Swainson's thrush

Work by Kristen Ruegg and colleagues (Ruegg and Smith 2002; Ruegg et al. 2006; Ruegg 2008):

Photo by D. Irwin

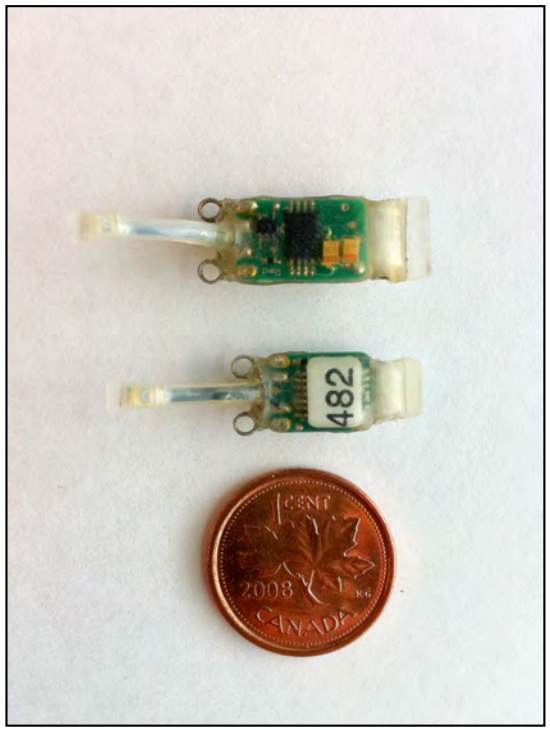




The tool: Geolocators

- First used on songbirds in 2007
  (Stutchbury et al. 2009; Purple Martins)
- Record time and light level throughout year
- Re-catch bird, download data to infer location throughout year

Photo by Kira Delmore



Is there a narrow migratory divide in Swainson's thrushes?

In June 2010, attached 39 geolocators at the edges of the hybrid zone

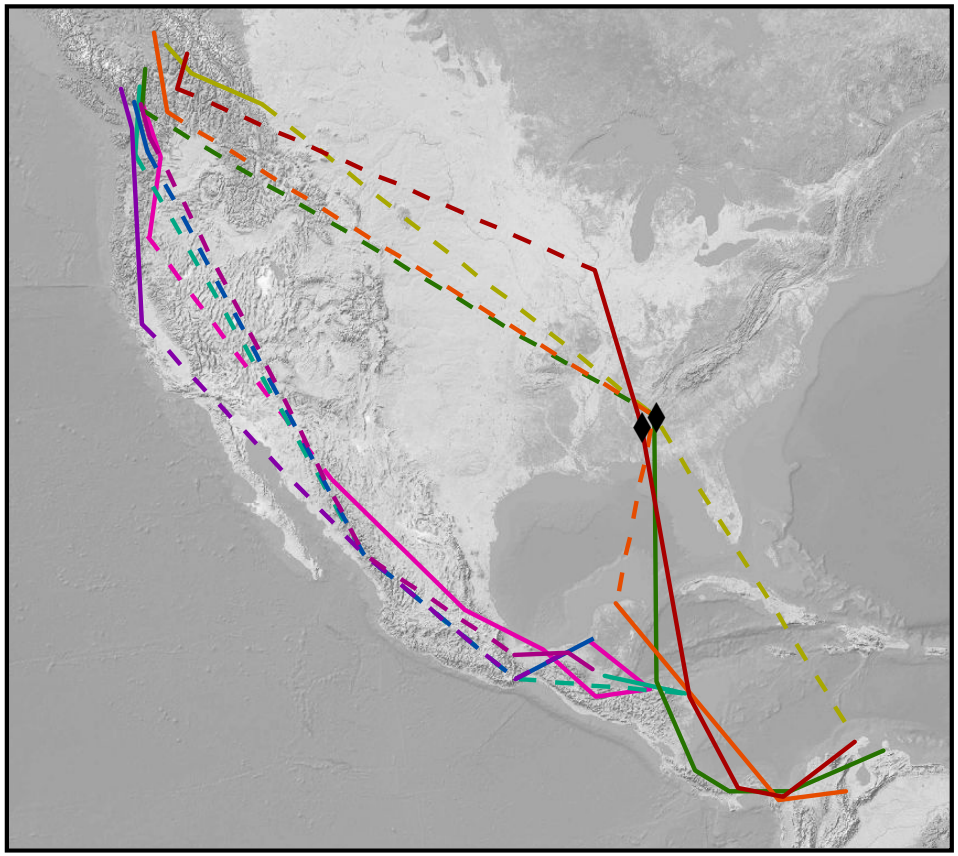
In 2011, recovered data from 9 (5 coastal and 4 inland)

Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators

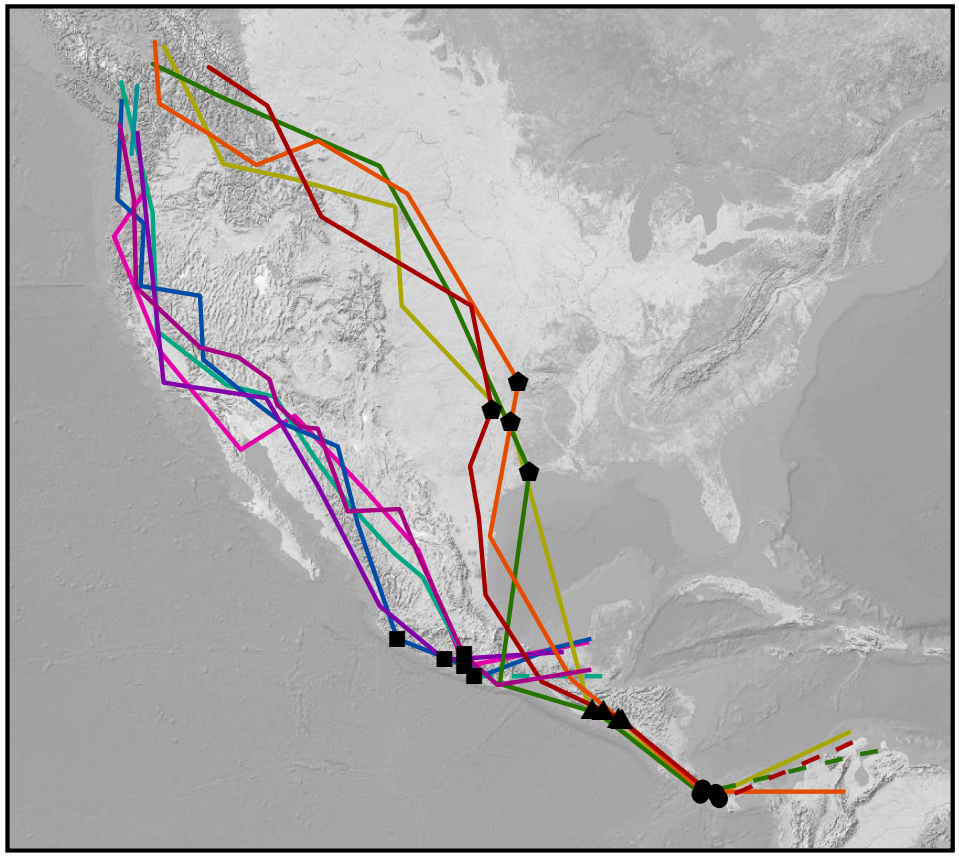
Kira E. Delmore, James W. Fox and Darren E. Irwin

Proc. R. Soc. B published online 26 September 2012
doi: 10.1098/rspb.2012.1229

Fall



Spring



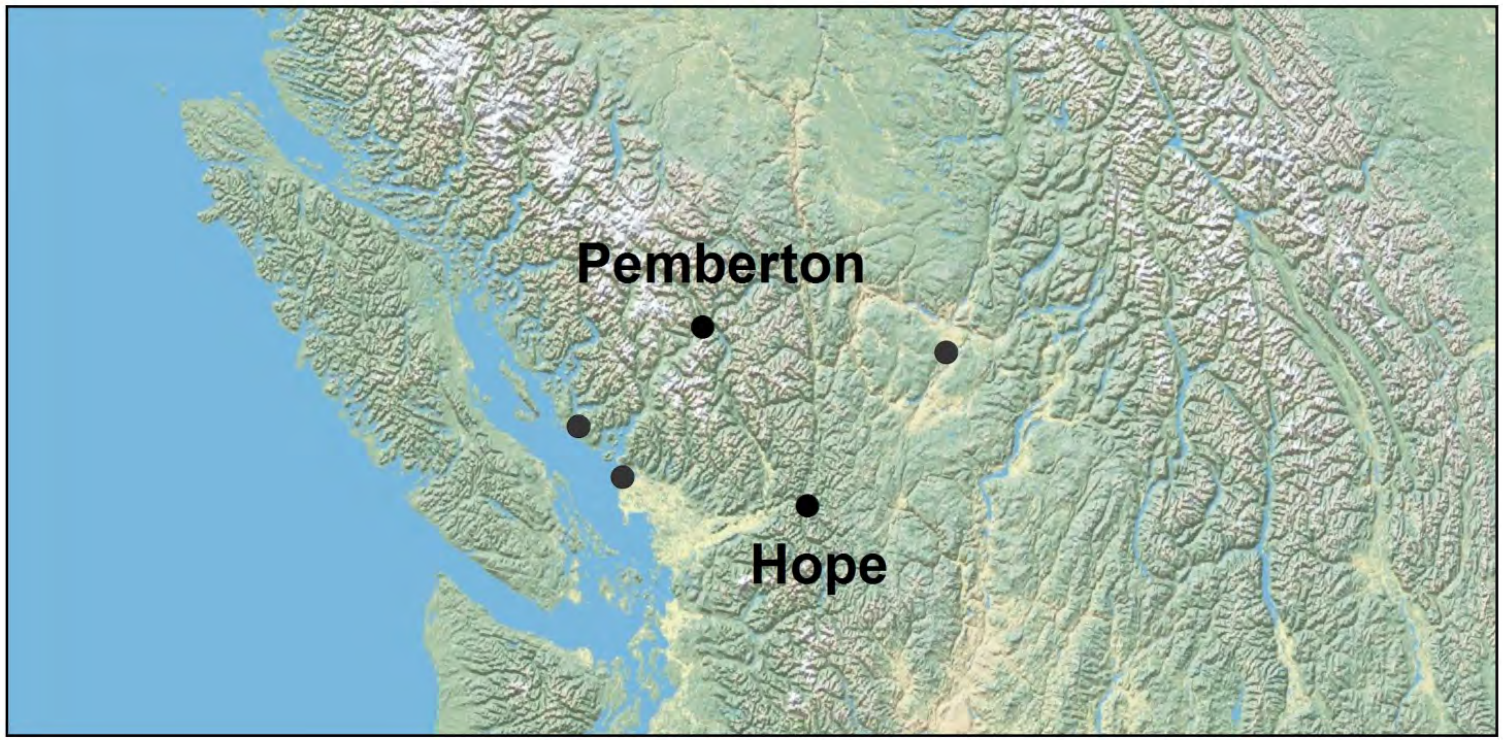
Dotted lines indicate times near the equinox when latitude is difficult to determine.

Is there a narrow migratory divide in Swainson's thrushes?

Yes

Do hybrids take intermediate routes?

In 2011, attached 58 geolocators at the center of the hybrid zone



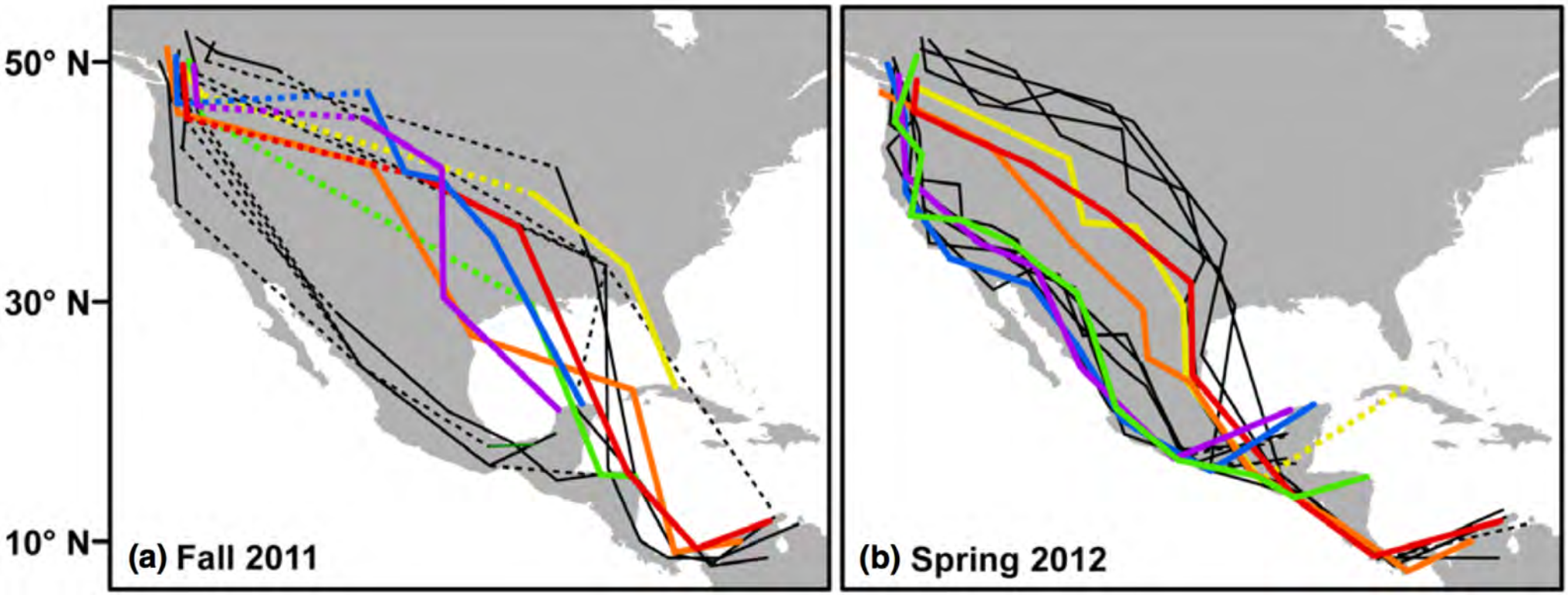
In 2012, Recovered data from 10 birds
Genotypes (based on 3 markers):
1 coastal, 3 inland, 6 hybrids

Routes of hybrid-zone birds with hybrid genotypes

(black lines show allopatric routes)

Fall

Spring

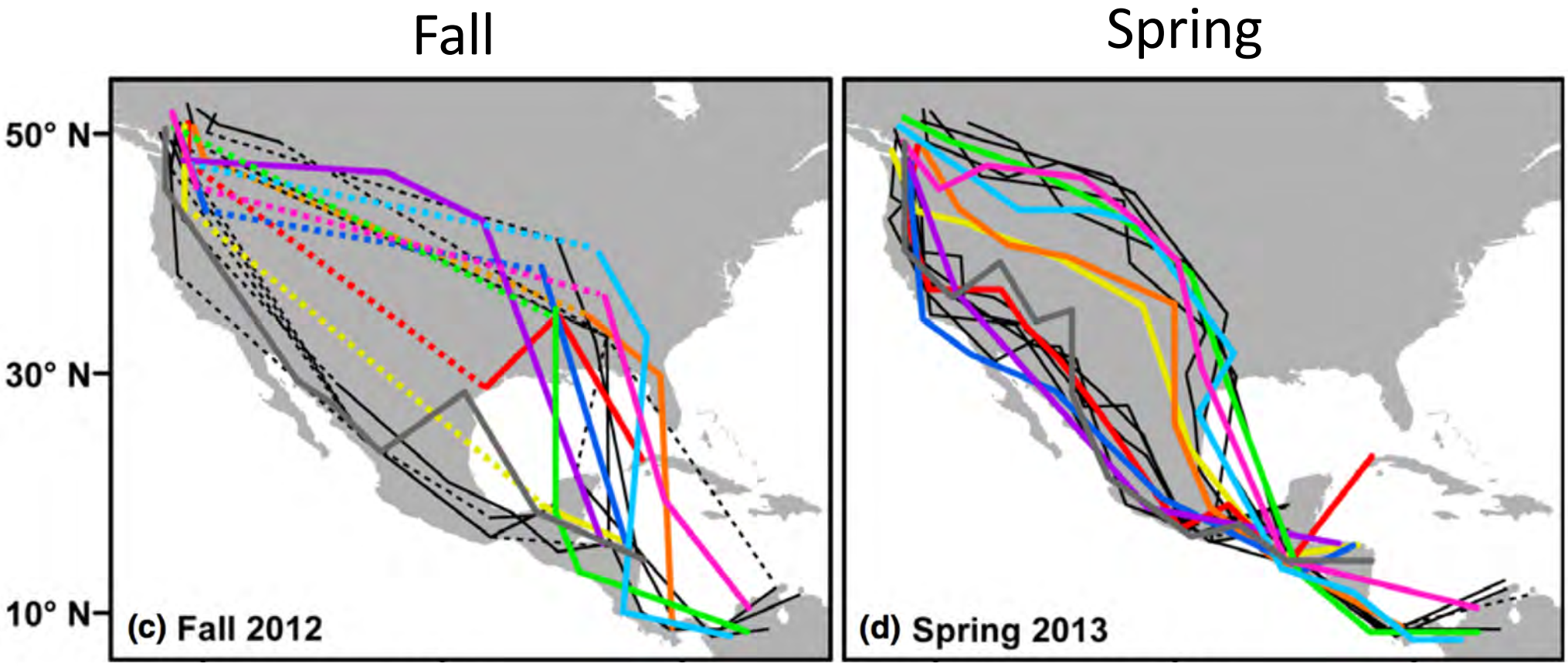


Some intermediate; some “mixed”

Delmore & Irwin 2014, *Ecology Letters*

Similar pattern in the next year

(11 recoveries, 9 with hybrid genotypes)



Some intermediate; some “mixed”

Delmore & Irwin 2014, *Ecology Letters*

Do hybrids really take intermediate routes?

Yes

Some routes are "mixed": an eastern route southward and a western route northward. Different genes for Fall and Spring?

So migratory route is a trait that:

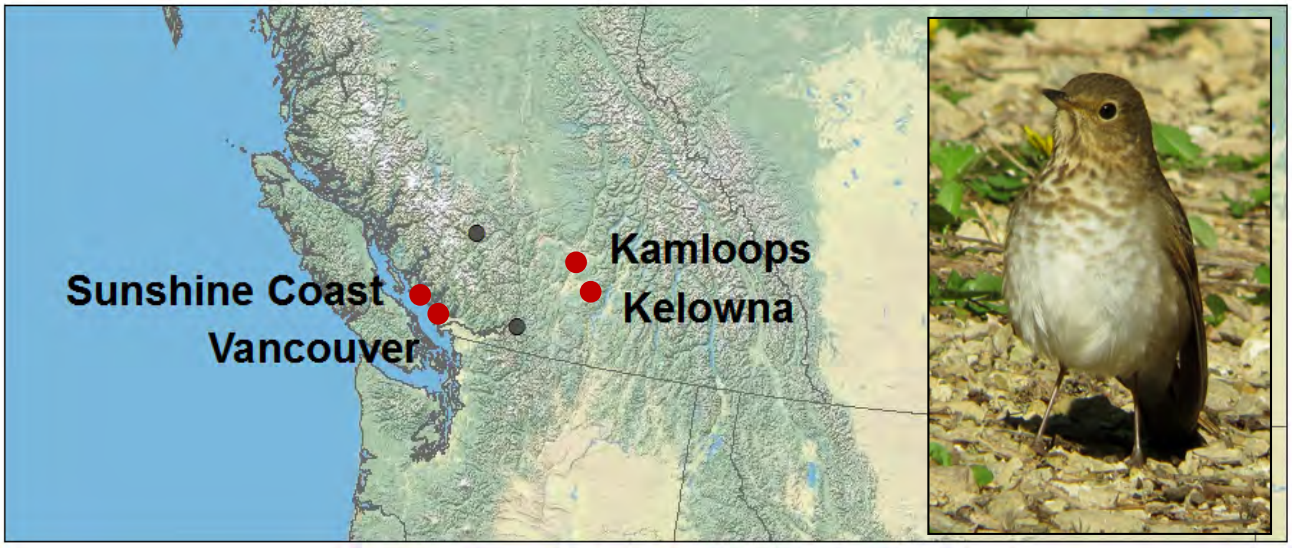
- Differs strongly between populations
- Is intermediate / mixed in hybrids
- Is likely inferior in intermediate form
- Is likely to have a strong genetic component

A key trait involved in speciation?

Can we find its genetic basis?

How much genomic differentiation is there between the migratory forms?

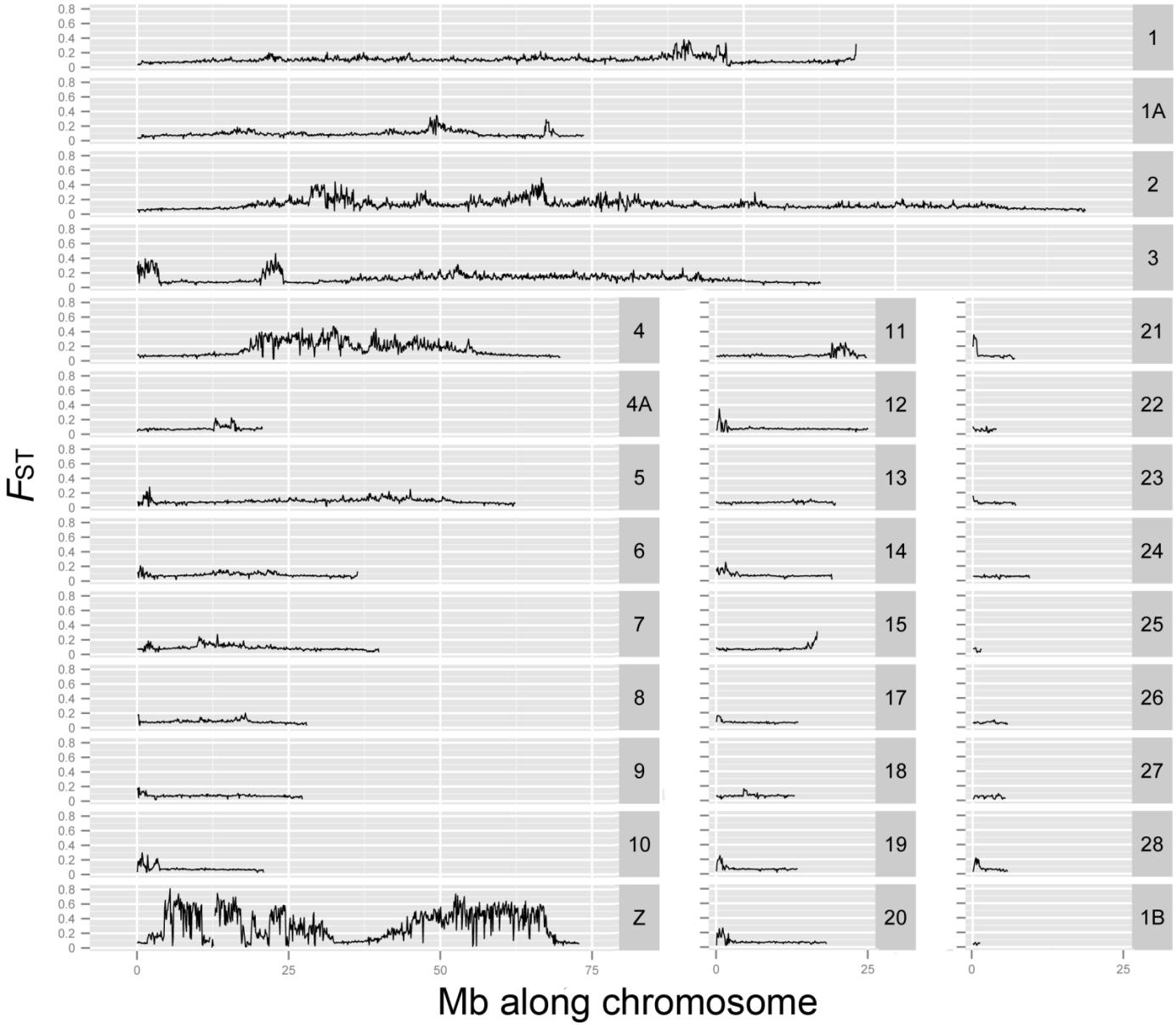
- Assembled a draft reference genome
- Examined genomic differences between pure forms



N = 10 individuals/population
Whole genome shotgun sequencing libraries
Detailed methodology in the paper

Delmore *et al*. 2015, *Mol. Ecol.*

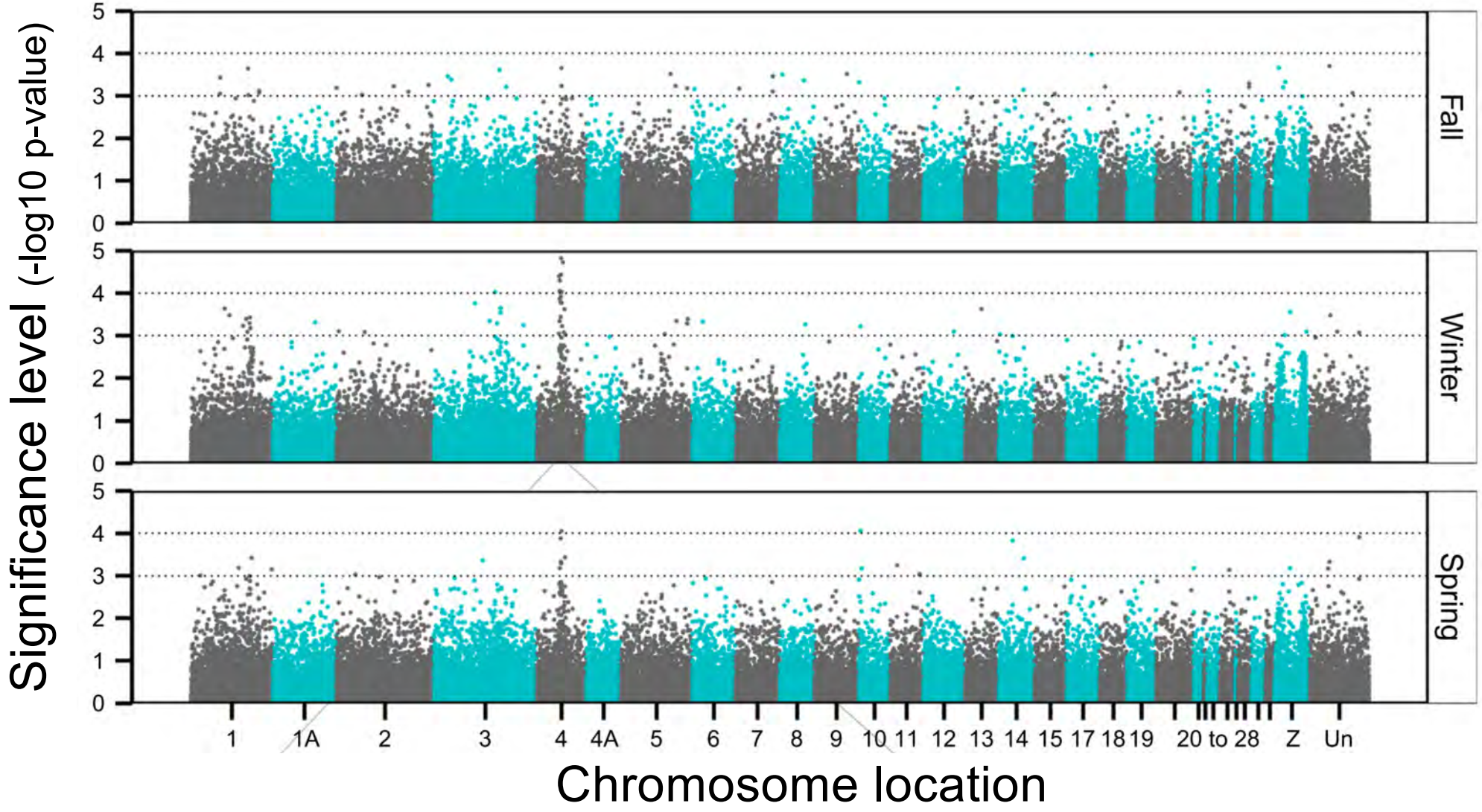
“Islands of genomic differentiation” between western and eastern Swainson’s thrush



Delmore *et al*. 2015, *Mol. Ecol.*

Genome-wide association between genotypes and migratory routes

(60k Genotype-By-Sequencing SNPs)



Delmore *et al*. 2016, *Current Biology*

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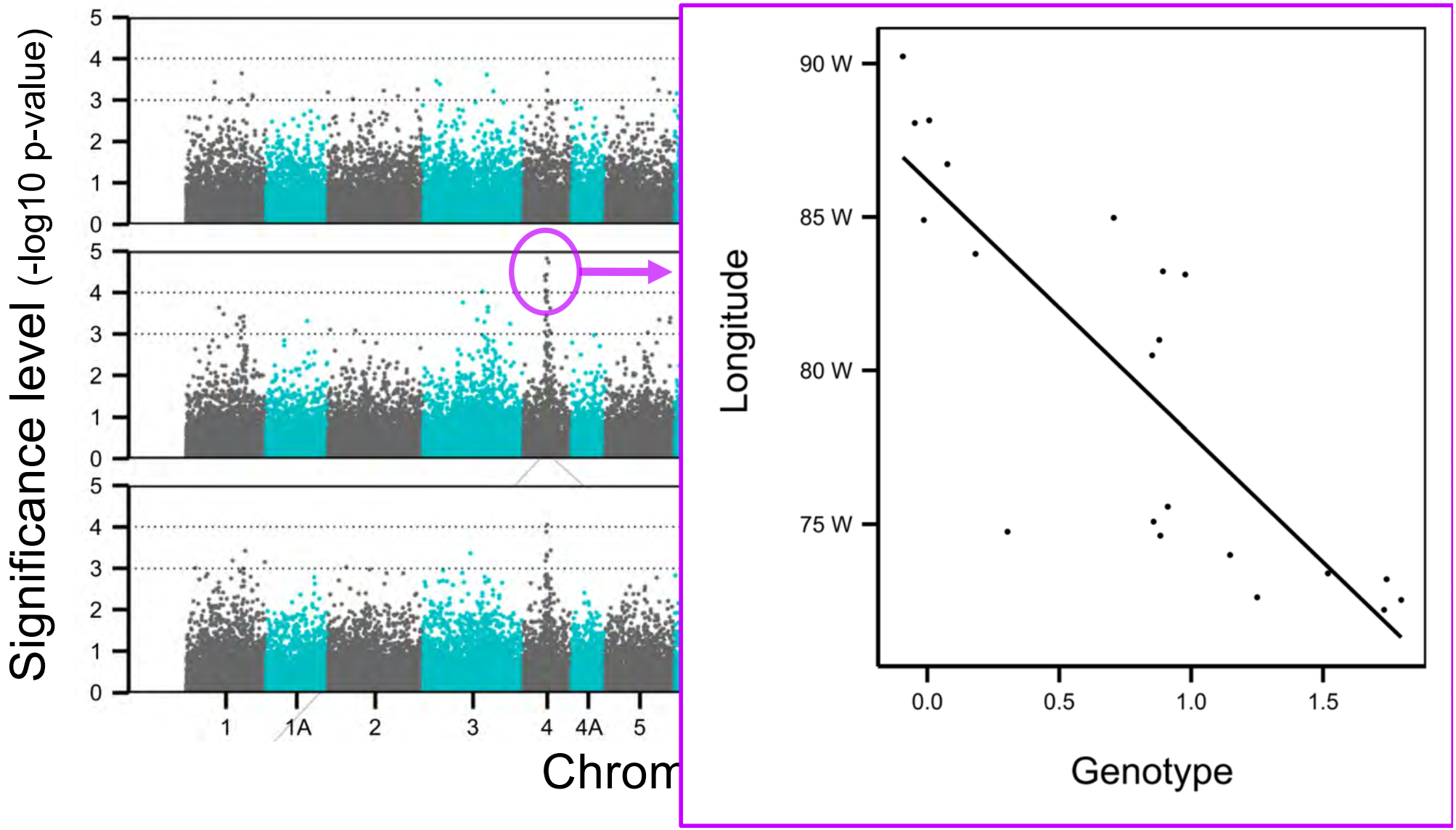
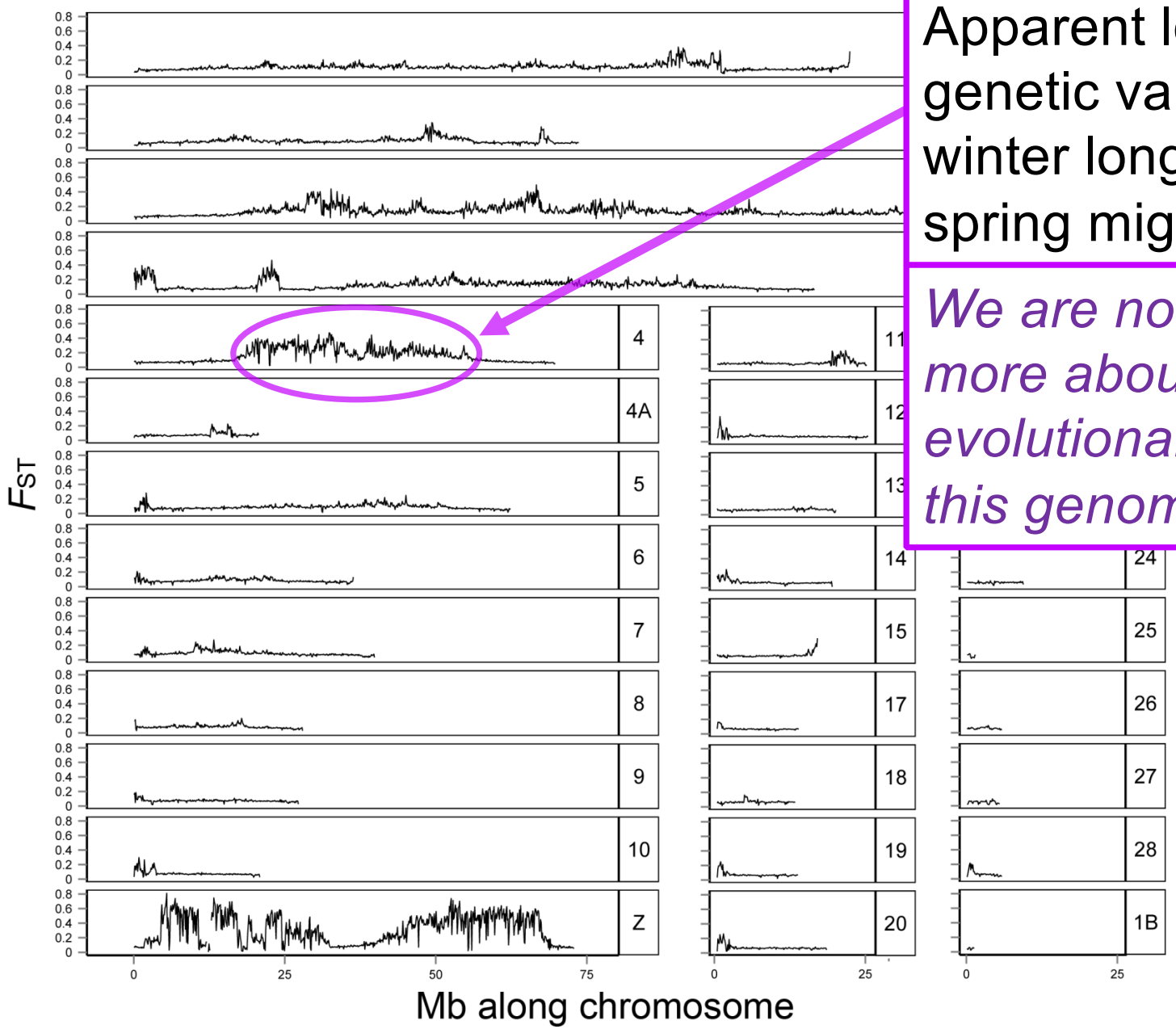


Delmore *et al*. 2016, *Current Biology*

Swainson's Trush genomic differentiation



Apparent location of genetic variation in winter longitude and spring migration routes

We are now learning more about the evolutionary history of this genomic region.

Delmore *et al*. 2015, *Mol. Ecol.*

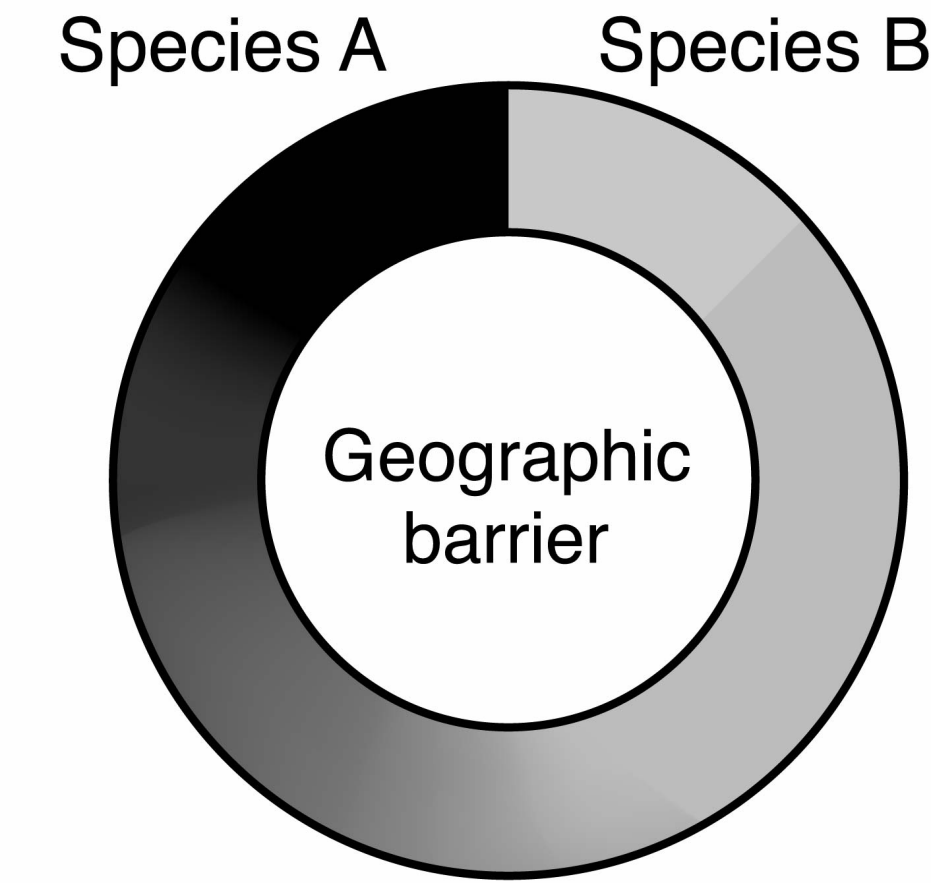
Part III: Genomic variation in the Greenish Warbler ring species

Miguel Alcaide, Liz Scordato, Trevor Price, Darren Irwin

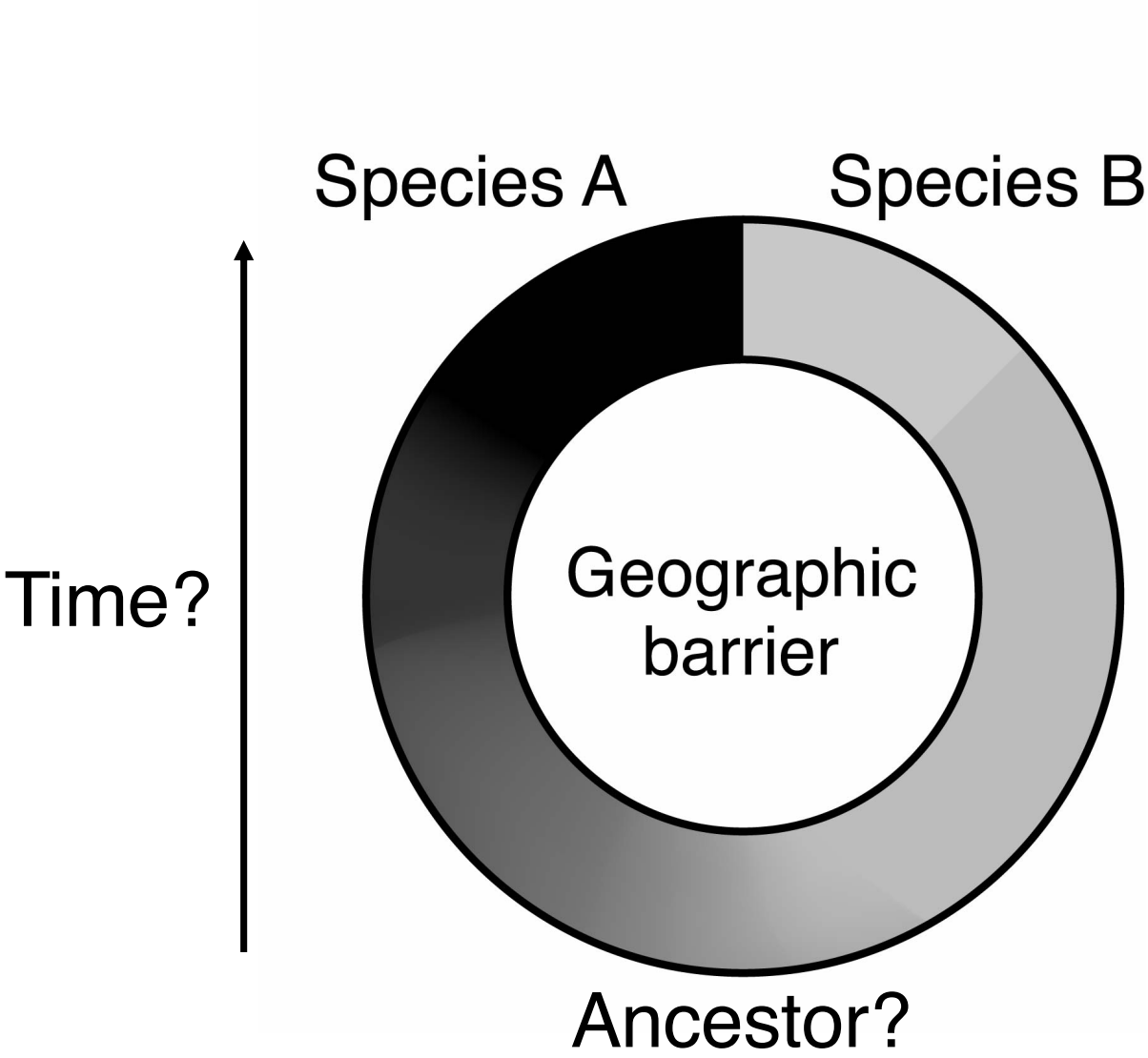
Ring Species:

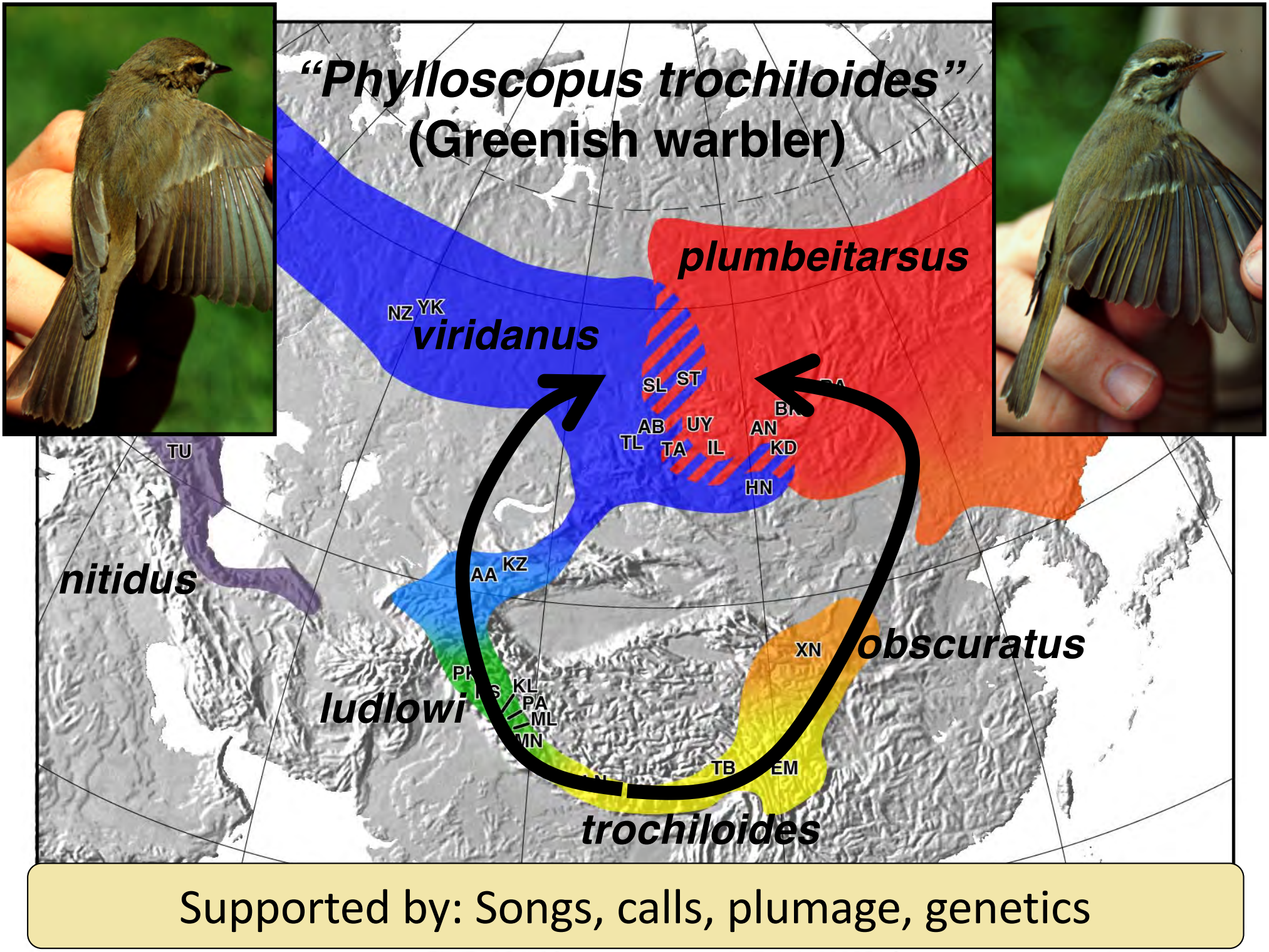
A ring of populations with a single species boundary.

"The perfect demonstration of speciation" (Ernst Mayr)



In a ring species, space may represent time.

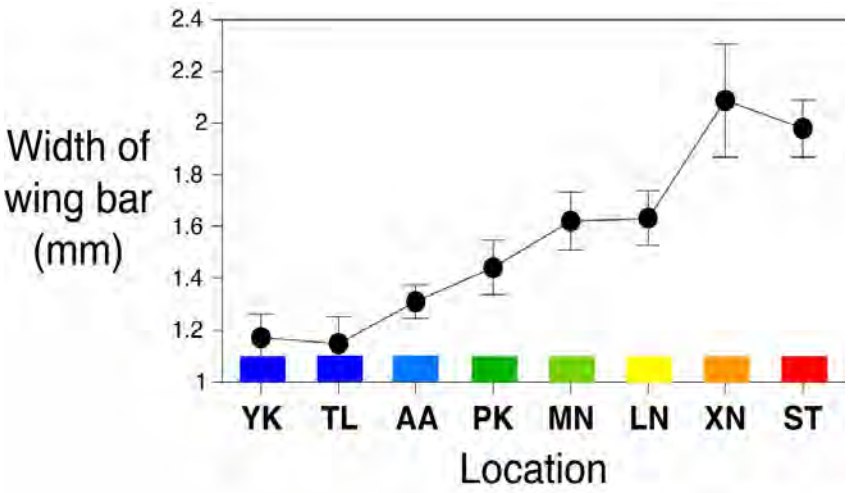




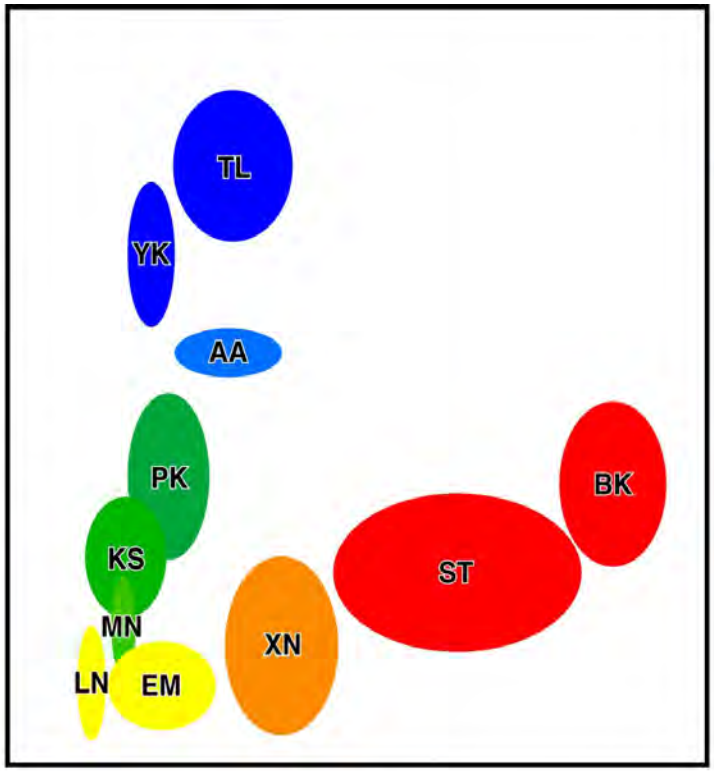
Supported by: Songs, calls, plumage, genetics

Phenotypic variation around the ring

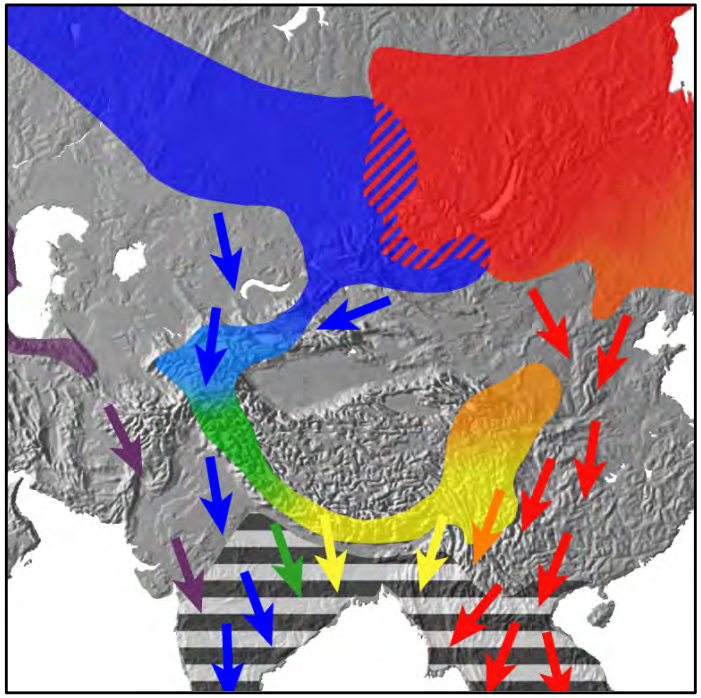
Plumage



Song



Migration



Genomic relationships around the ring (134 individuals, 580k SNPs)

History of varying amounts of gene flow around the west, south, and east sides of the ring

East Siberia

West Siberia

Central Asia

West Himalayas

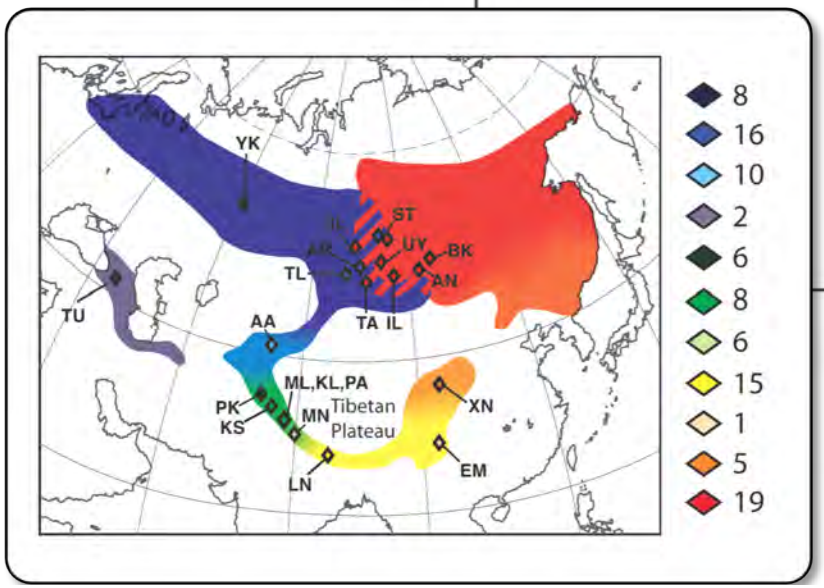
Central Himalayas

China

Nepal

PC1

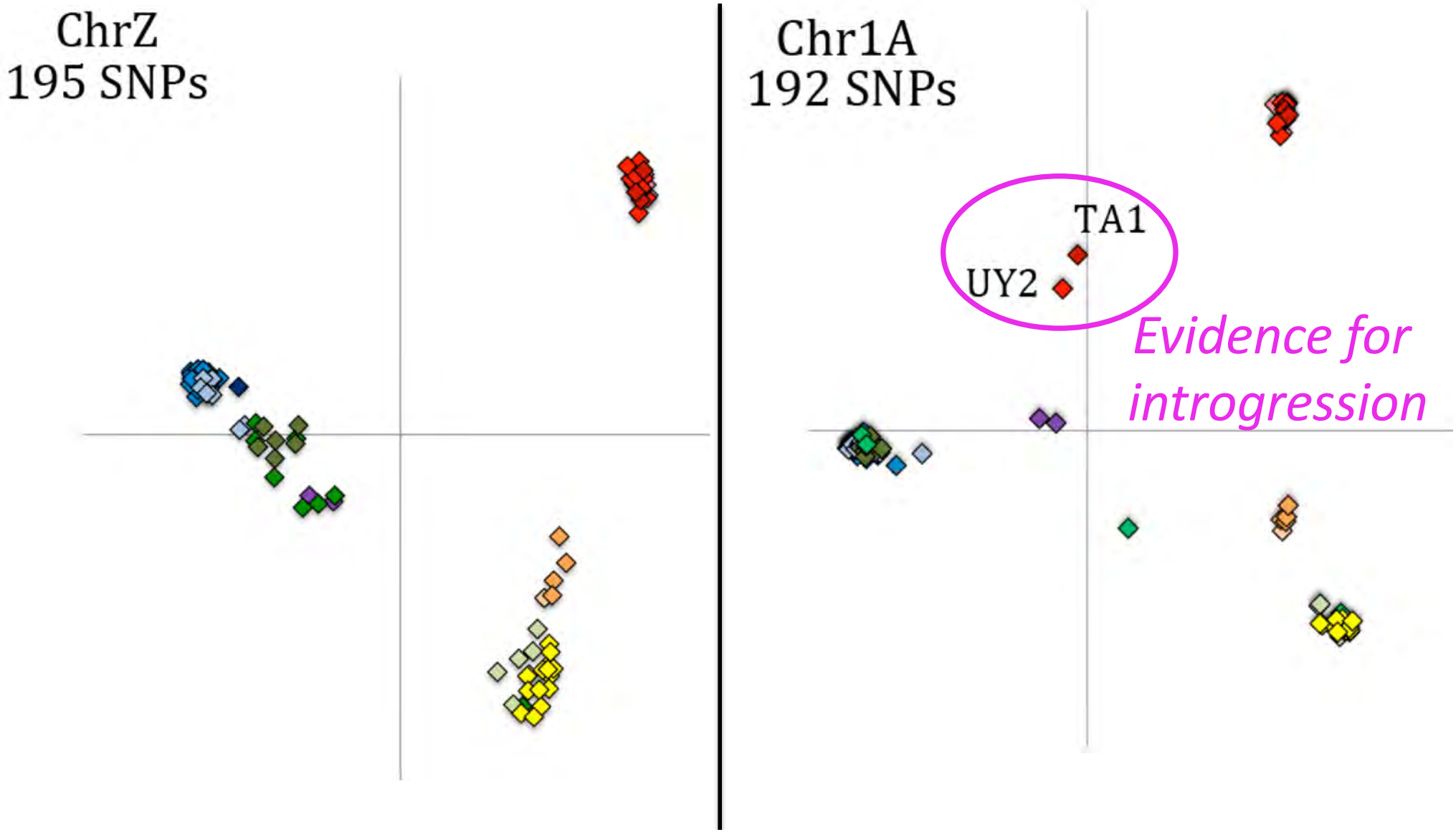
PC2

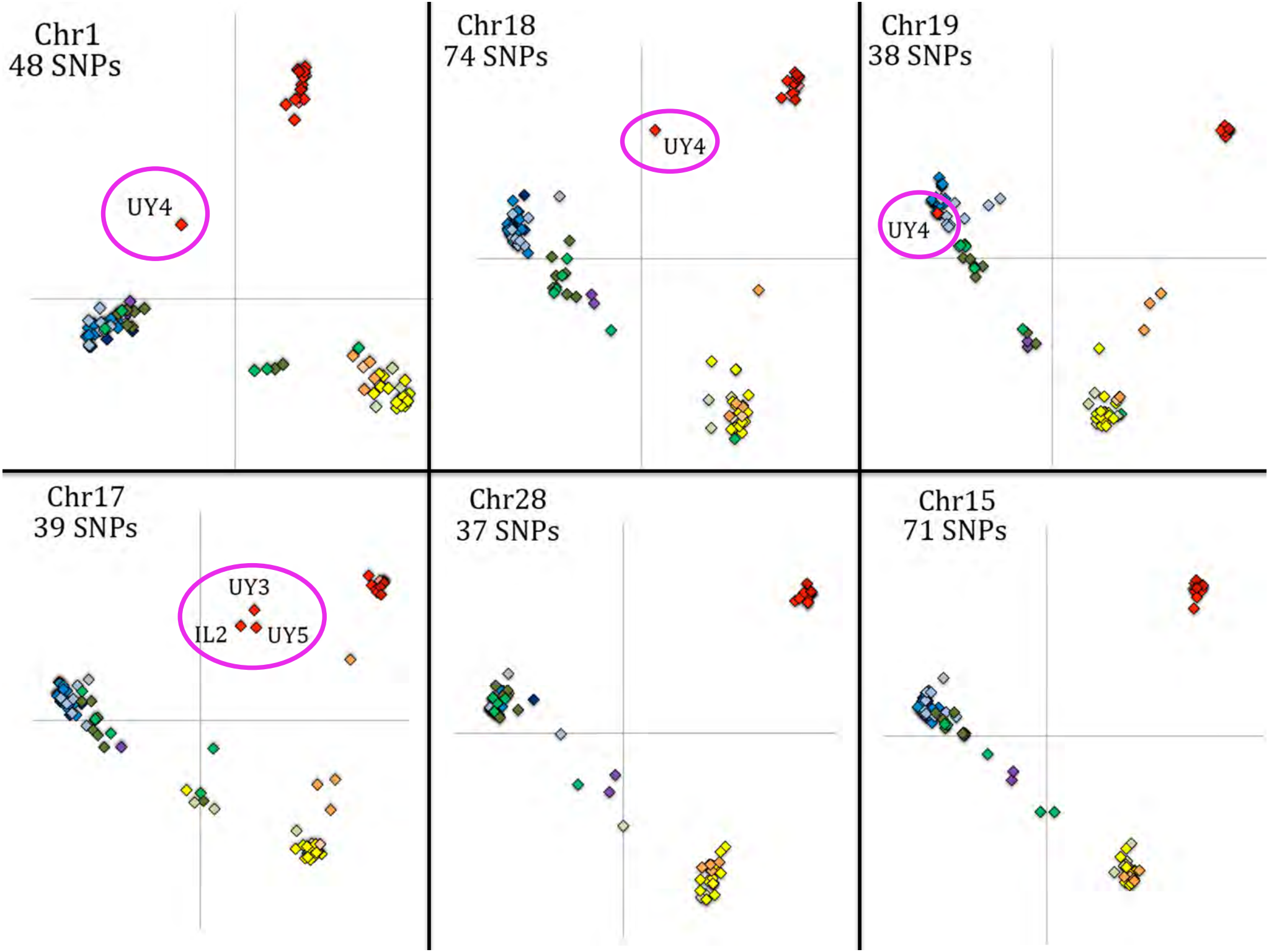


Alcaide et al.(2014) *Nature*; Irwin et al. 2016 *Mol. Ecol.*

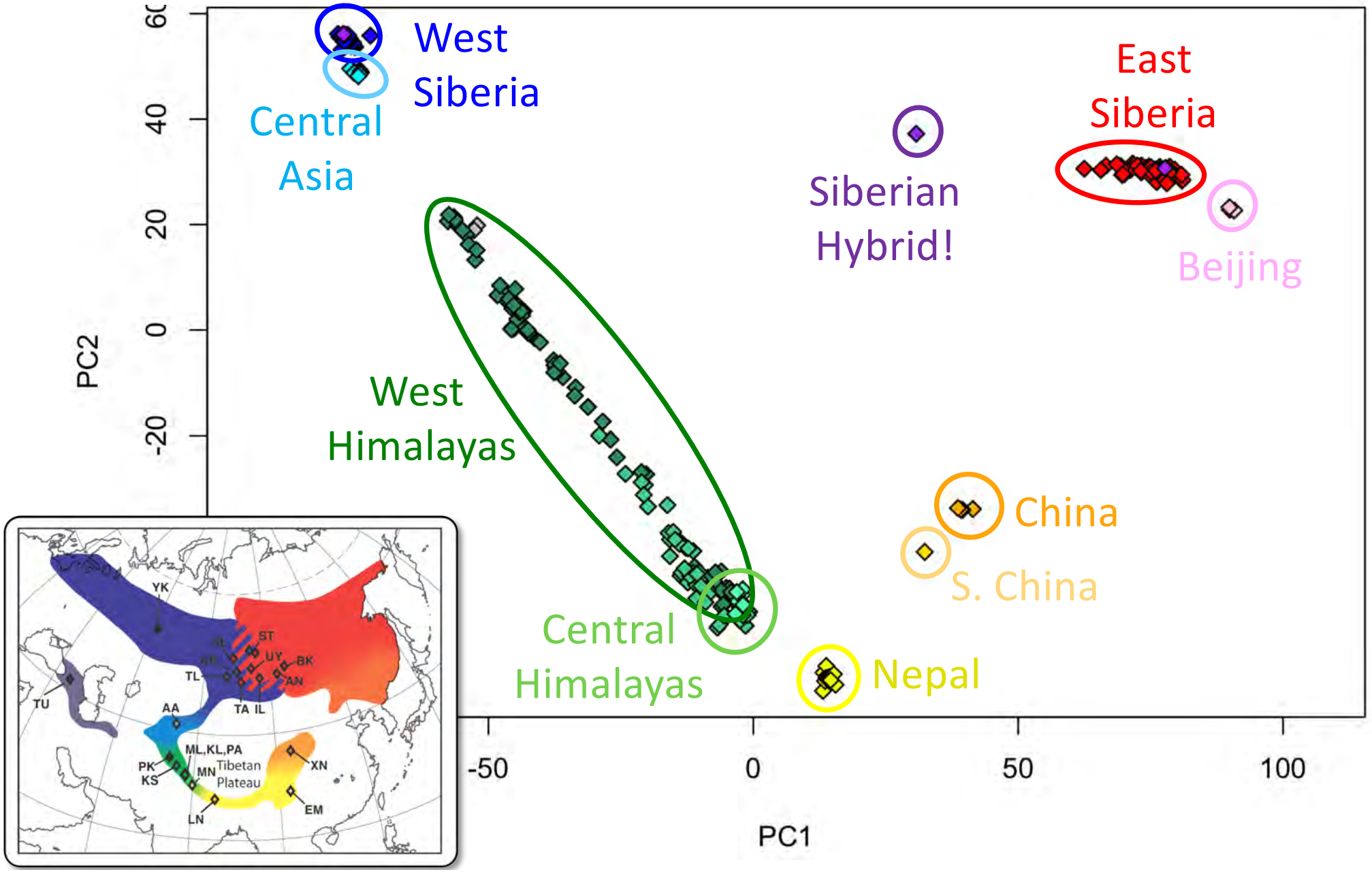
Per-chromosome relationships

(based on highly divergent SNPs)




Chr1
48 SNPs
UY4
Chr18
74 SNPs
UY4
Chr19
38 SNPs
UY4
Chr17
39 SNPs
UY3
IL2
UY5
Chr28
37 SNPs
Chr15
71 SNPs

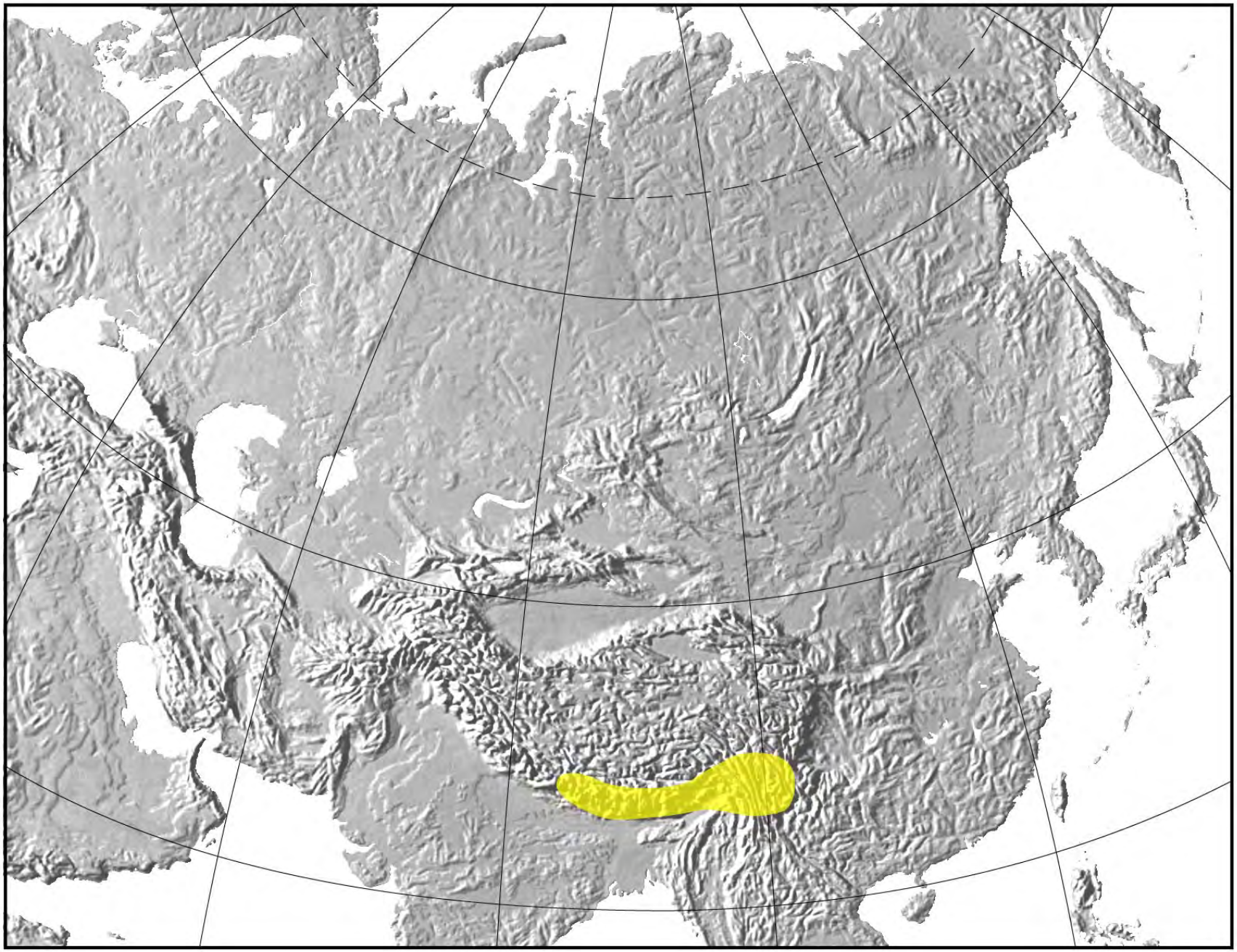
Brand new data from yesterday!
(260 individuals, 715k SNPs)



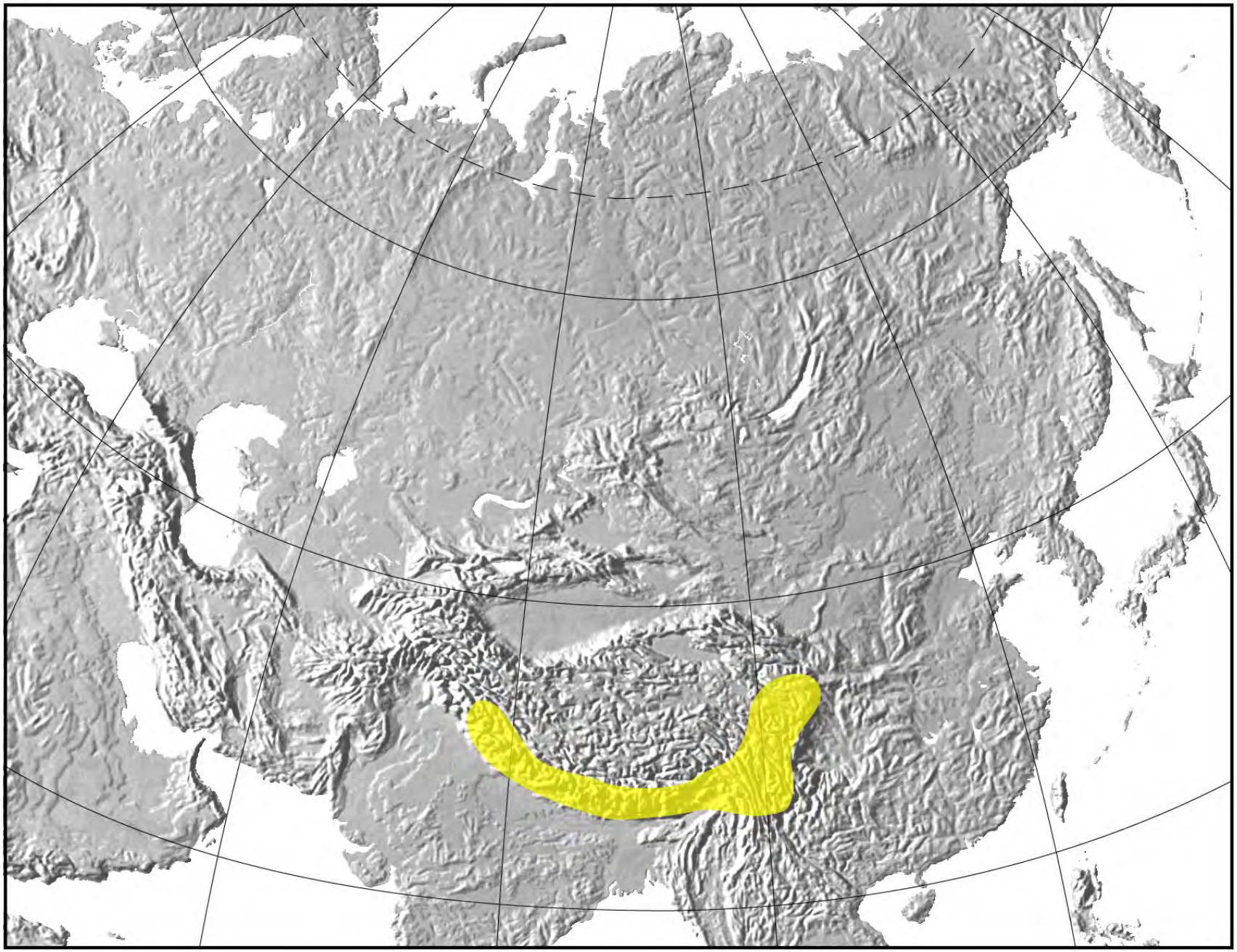
Conclusions from genomic analysis

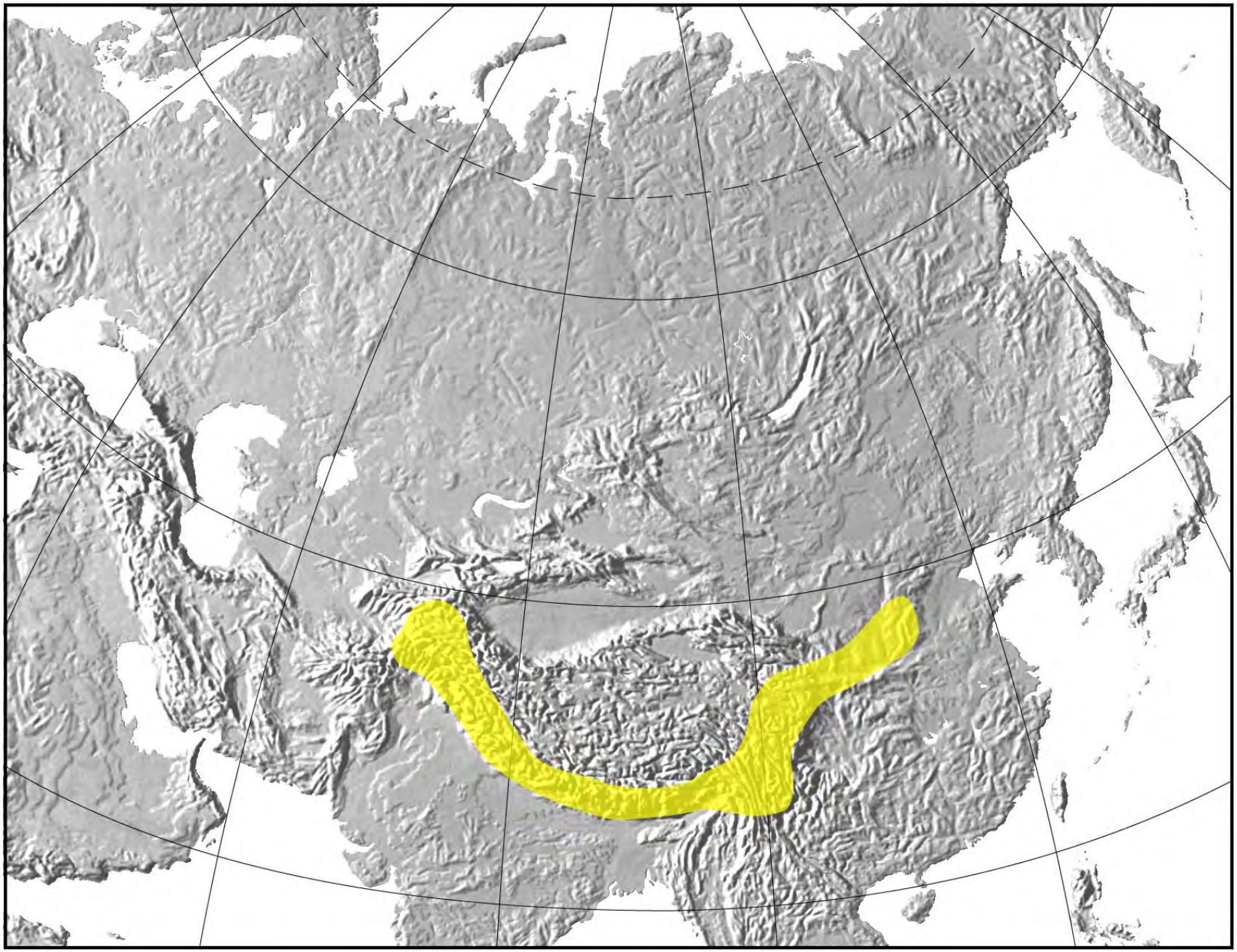
- Genomic variation in Greenish Warblers is consistent with the ring species concept : a ring of populations with a single location with strong reproductive isolation.
- Genomic clustering around ring suggests periods of allopatry and hybridization; not a good example of "speciation by distance" alone.
- Trickle of hybridization between terminal forms, but still highly distinct, with evidence for selective sweeps at divergence peaks.
- Patterns of RI remarkably consistent with patterns of phenotypic variation.

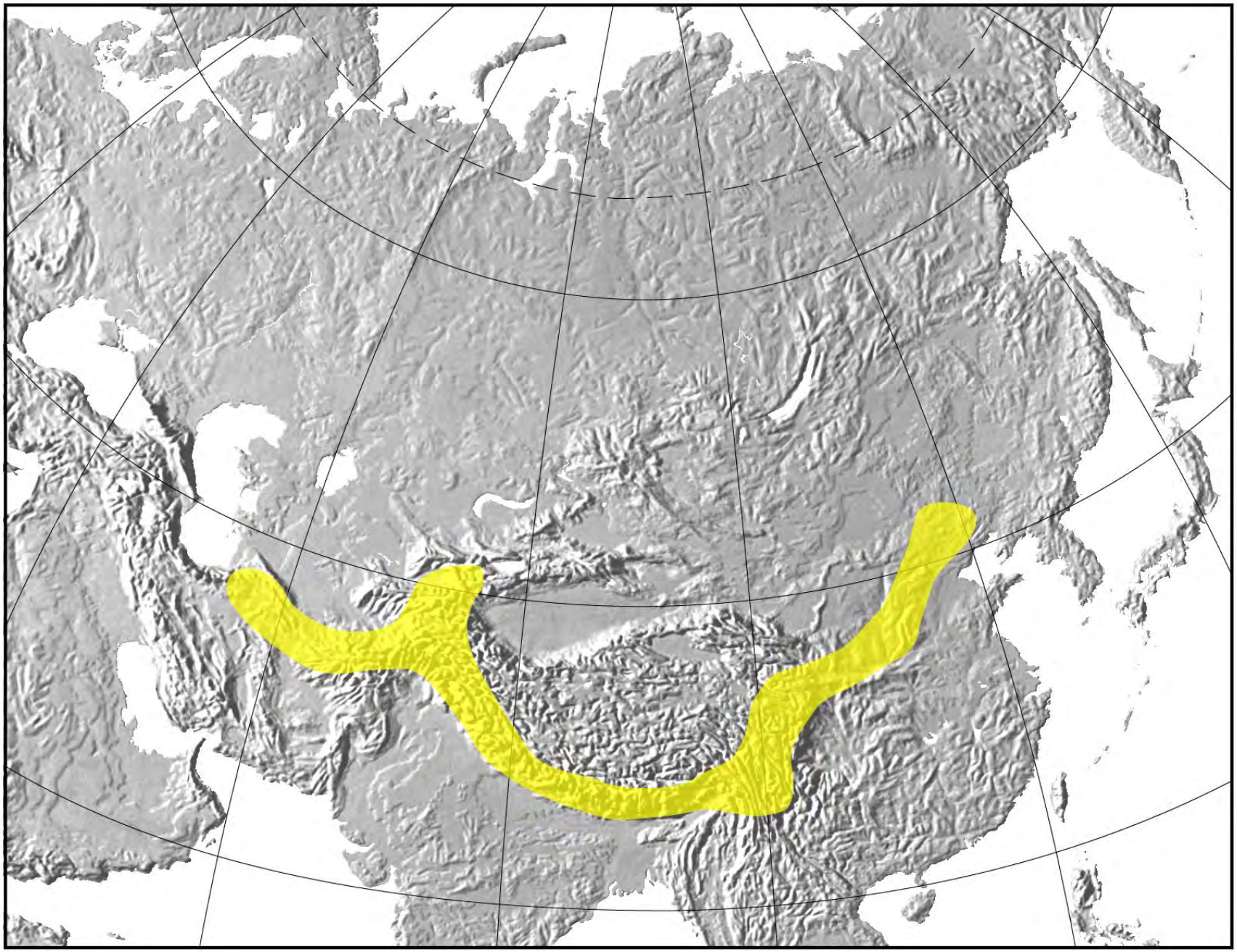
How did this situation arise?

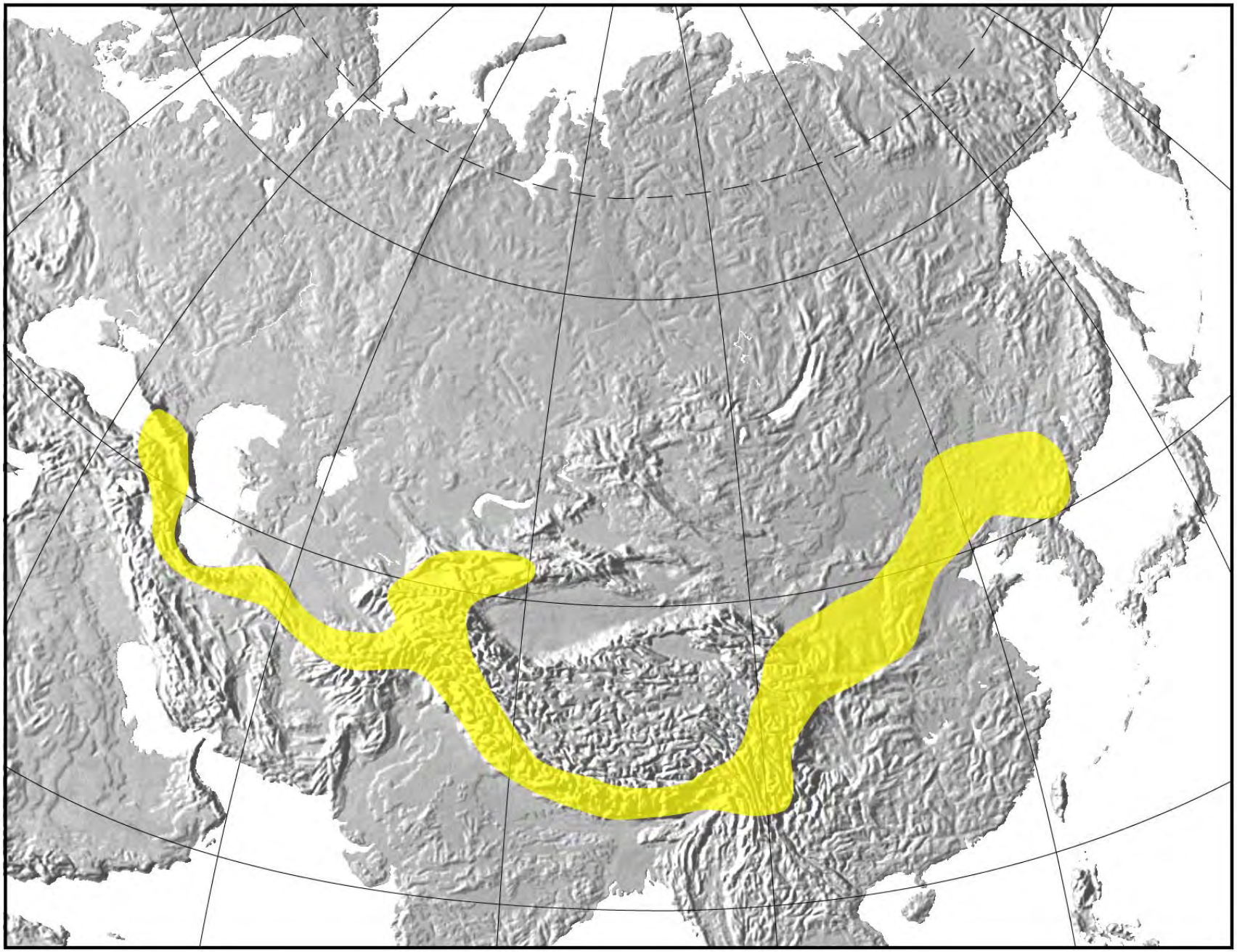


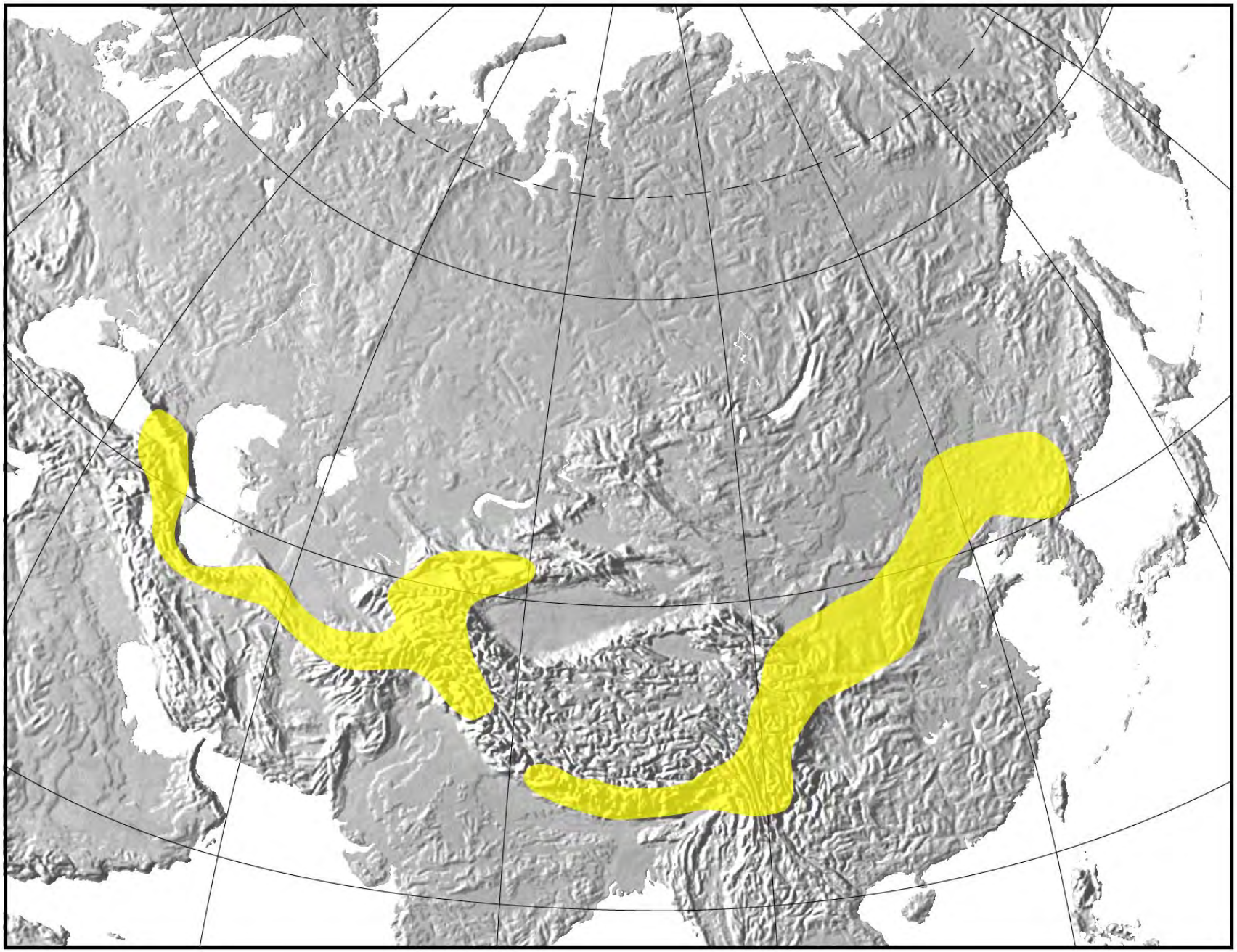
Roughly 2 million years ago

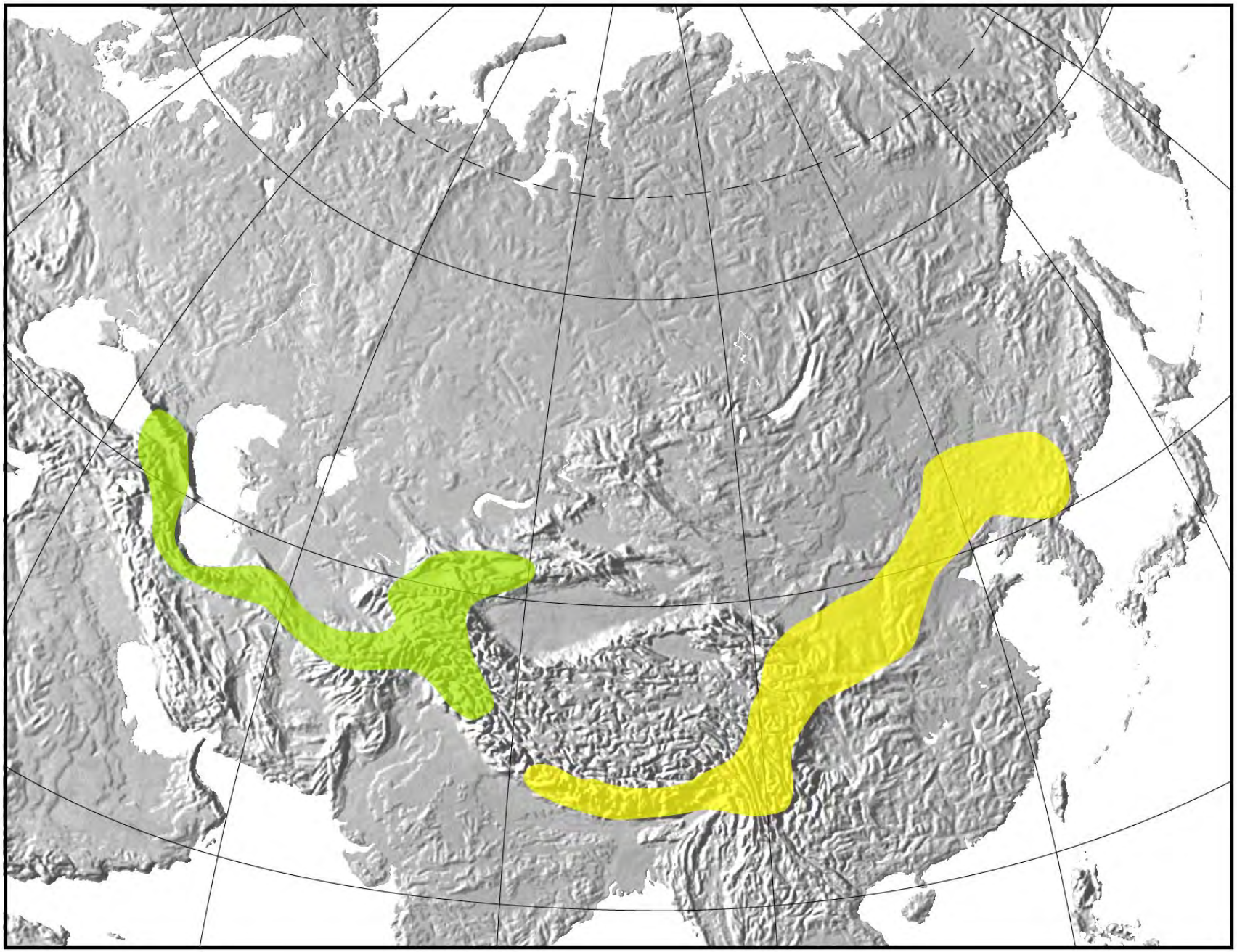


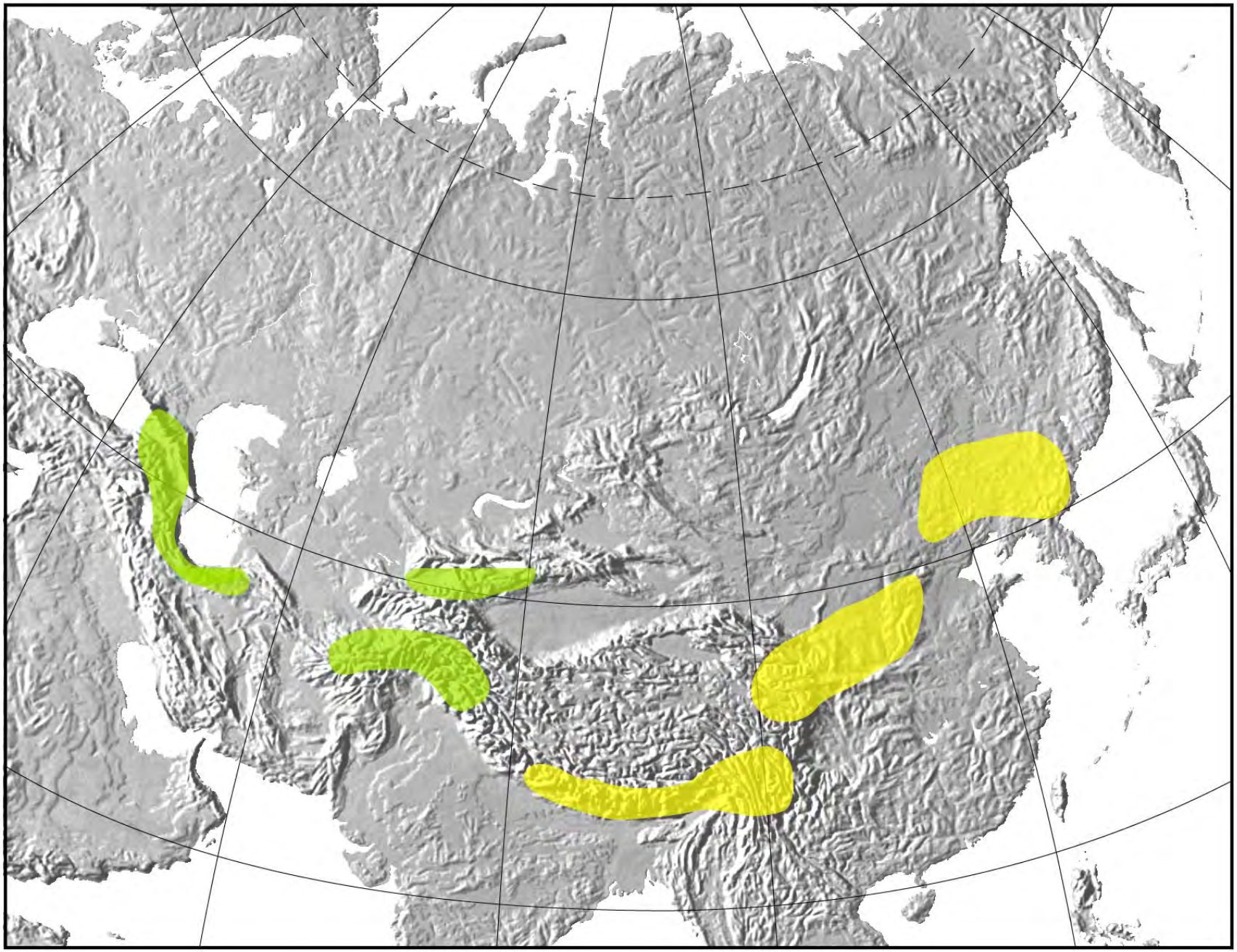


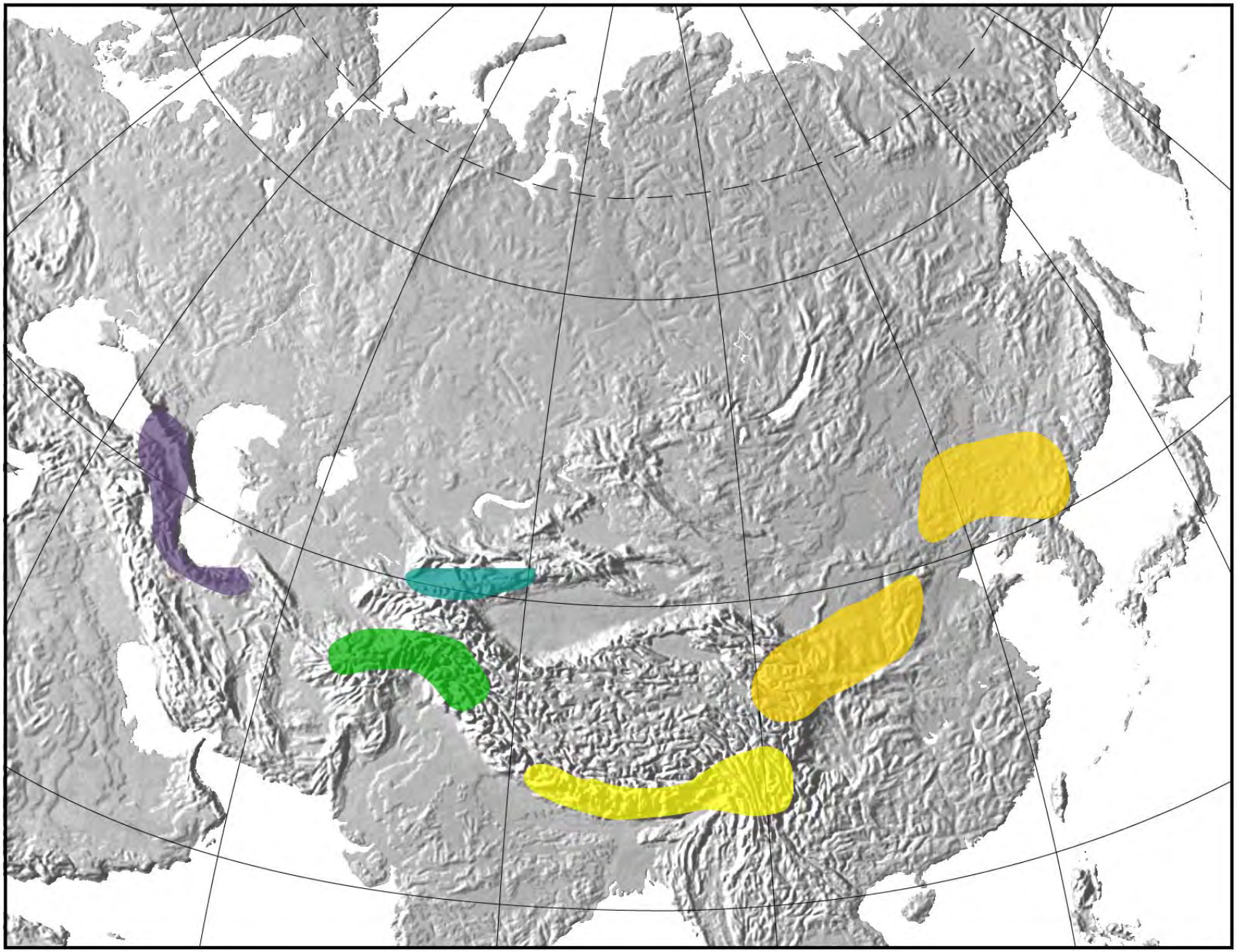


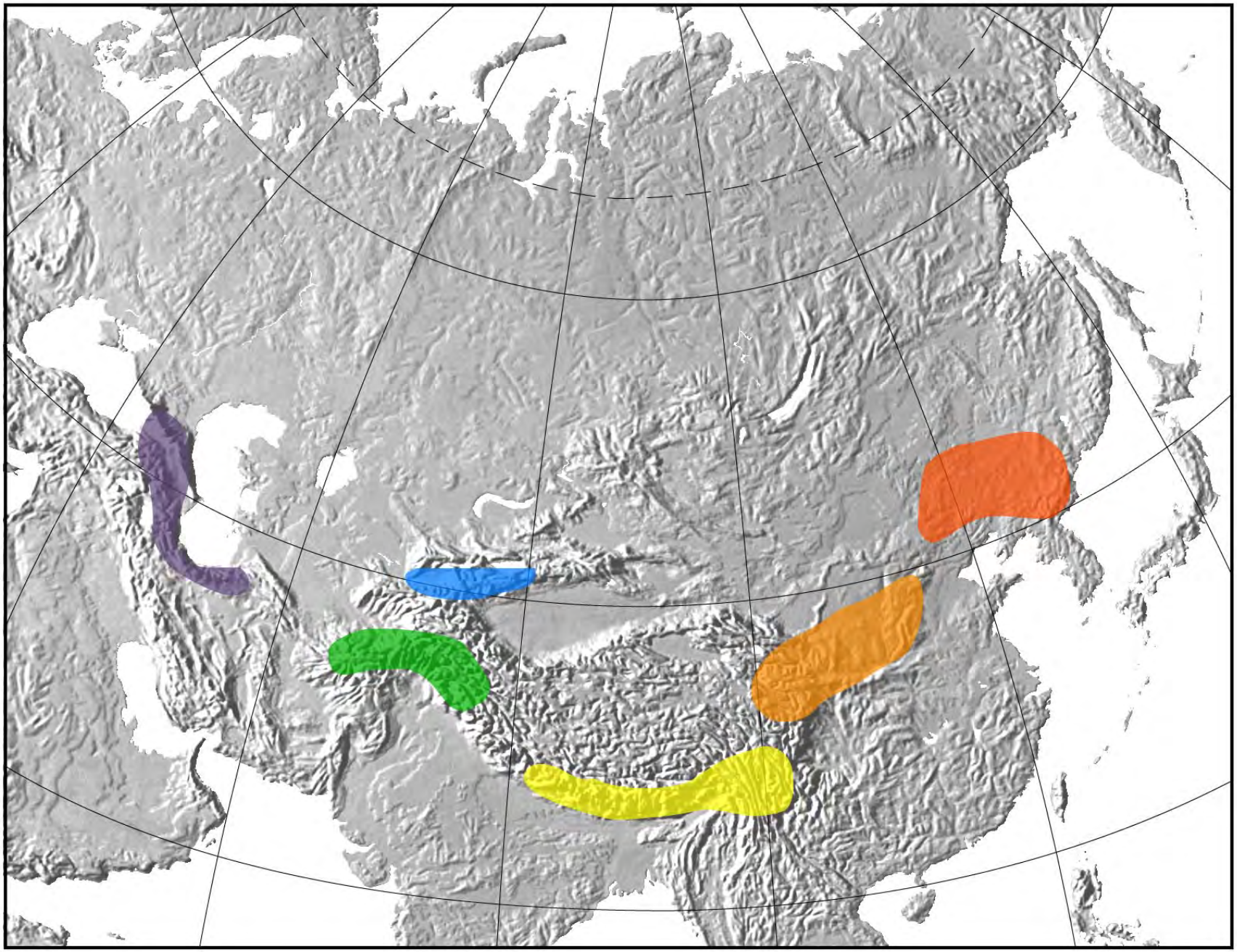


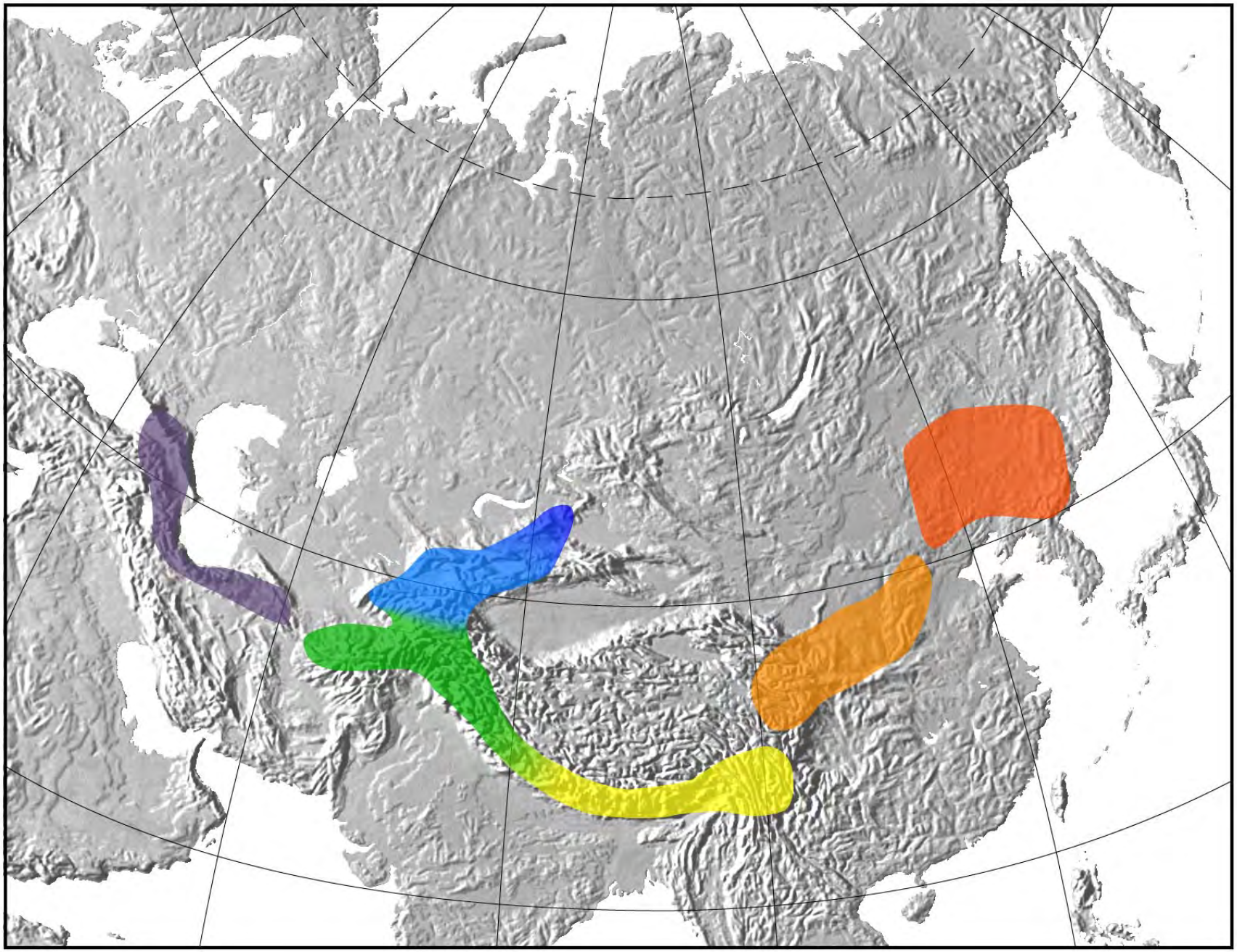


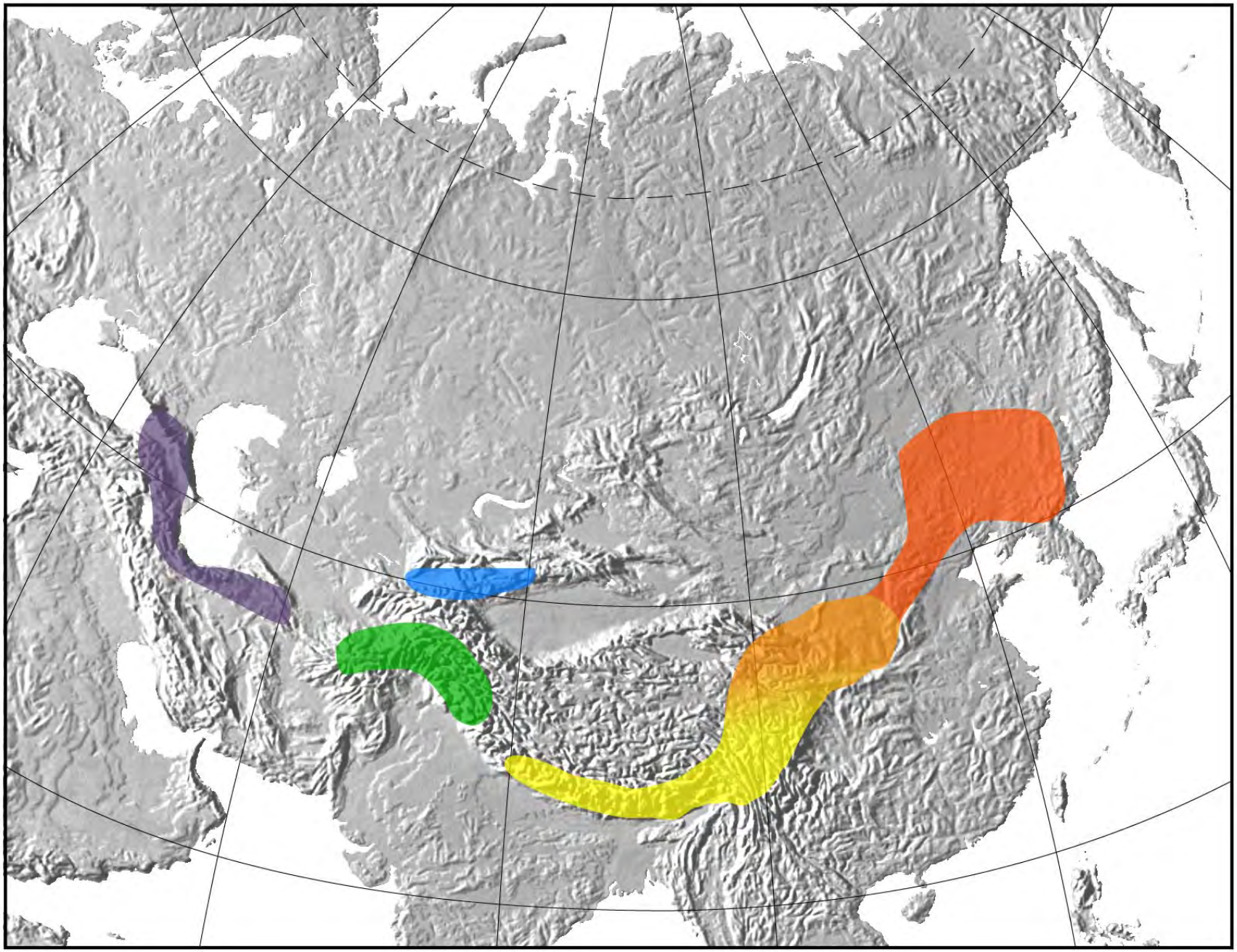


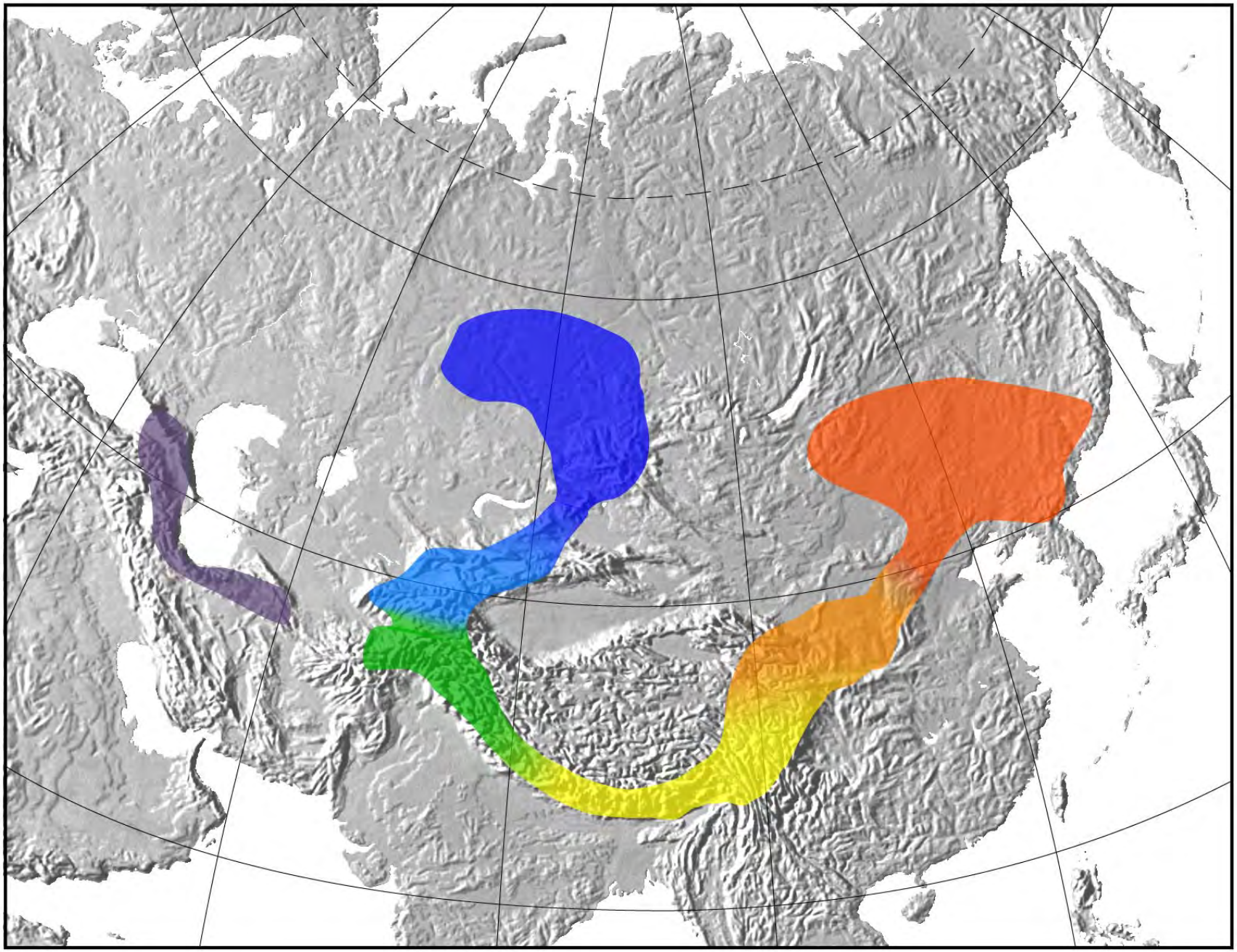


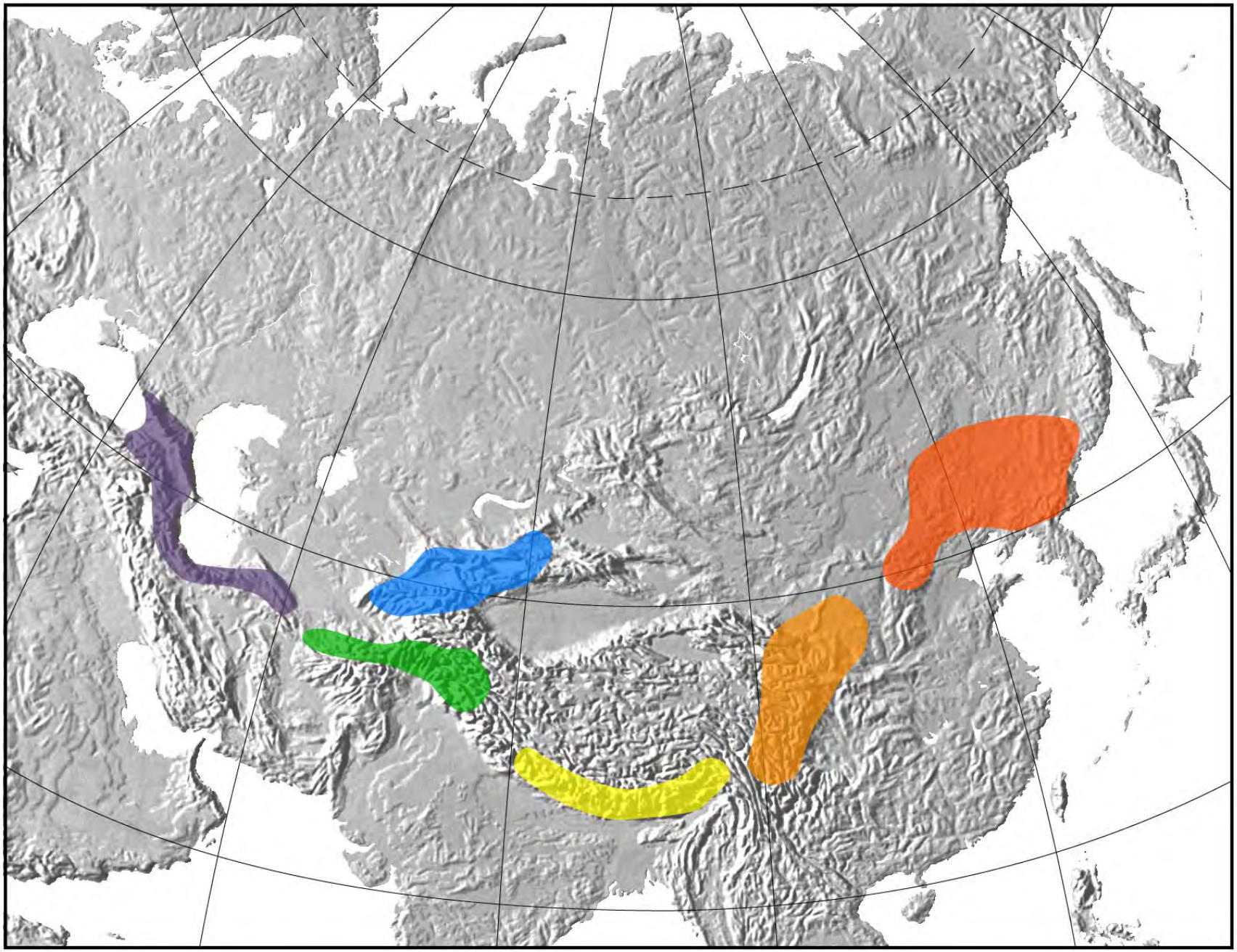


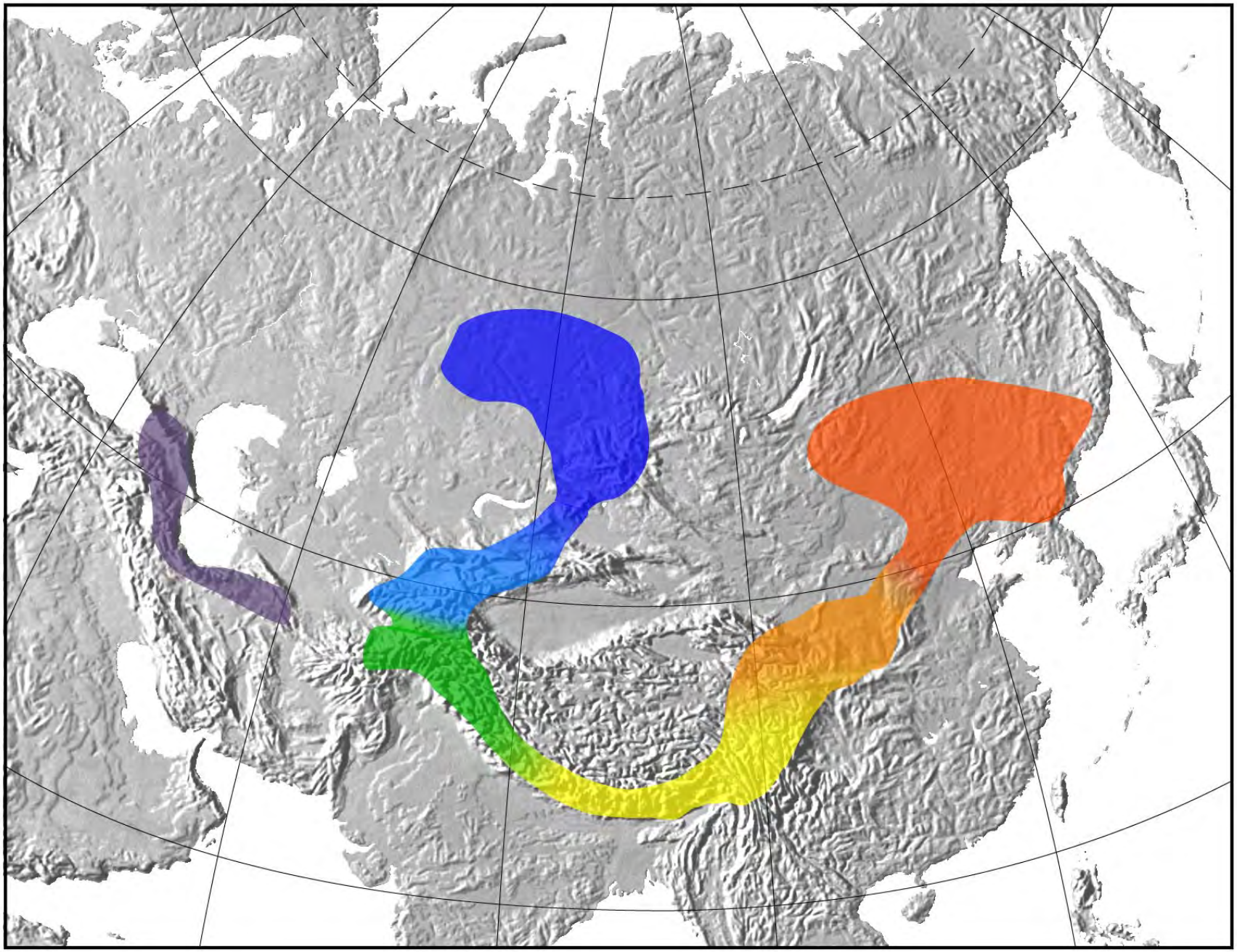


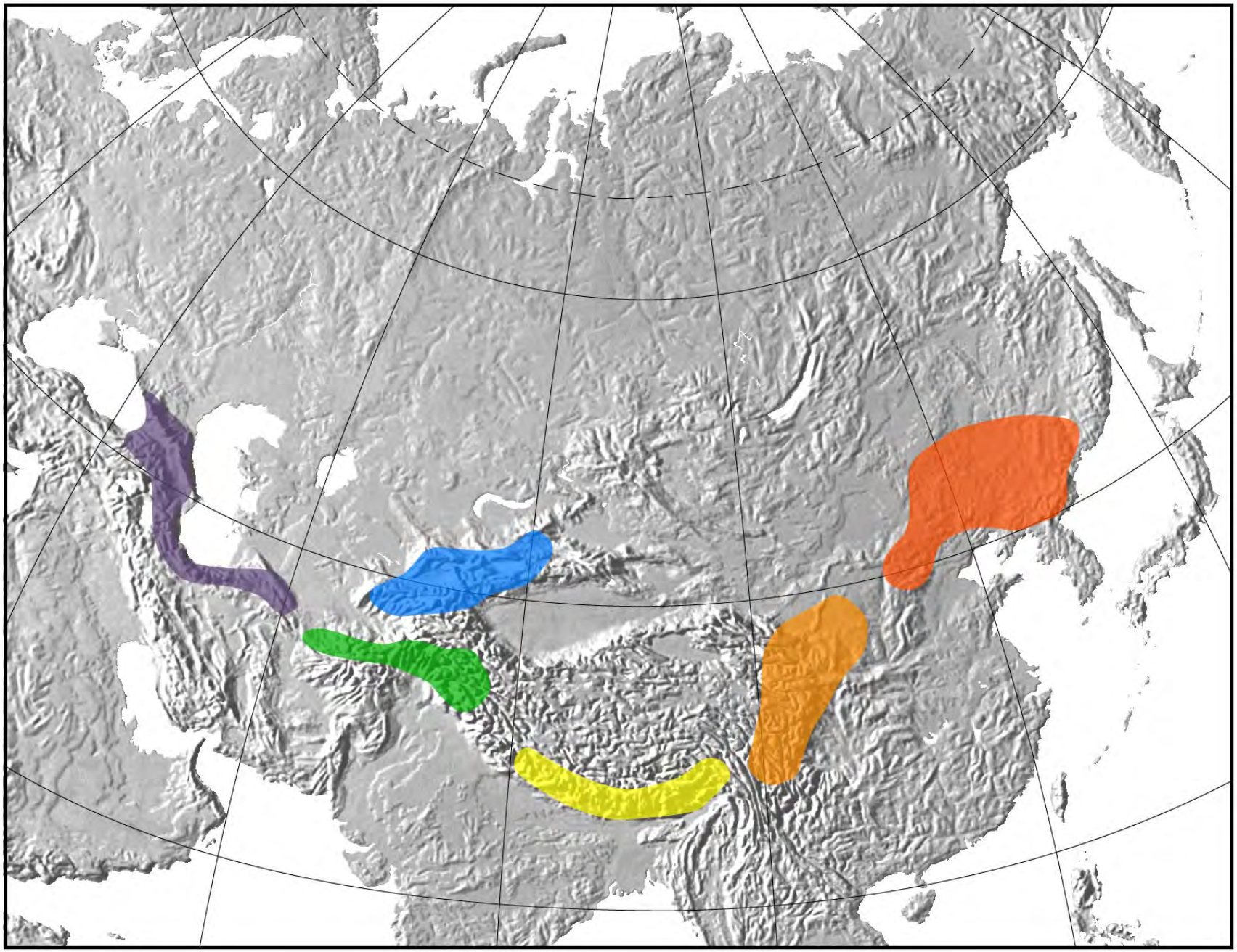


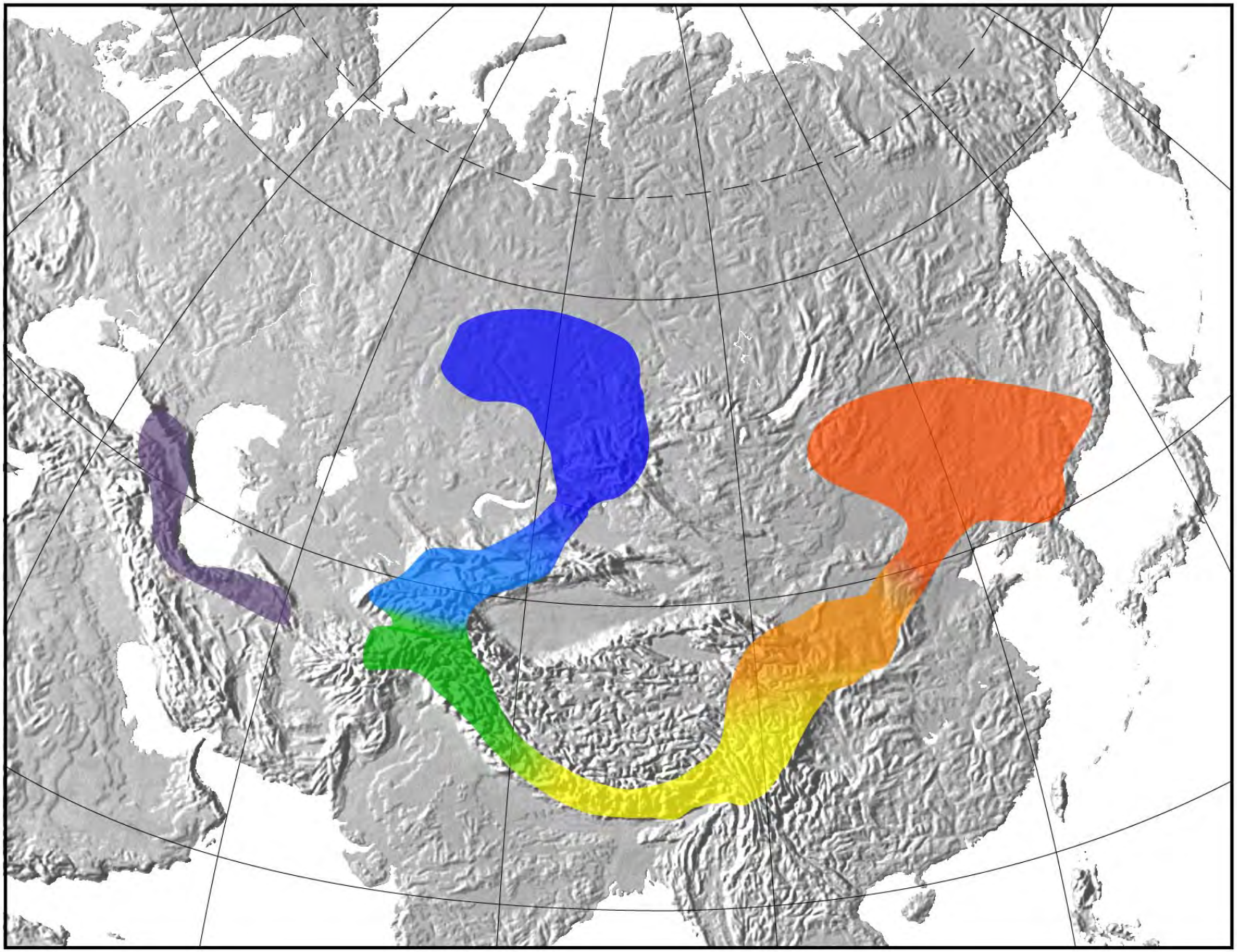


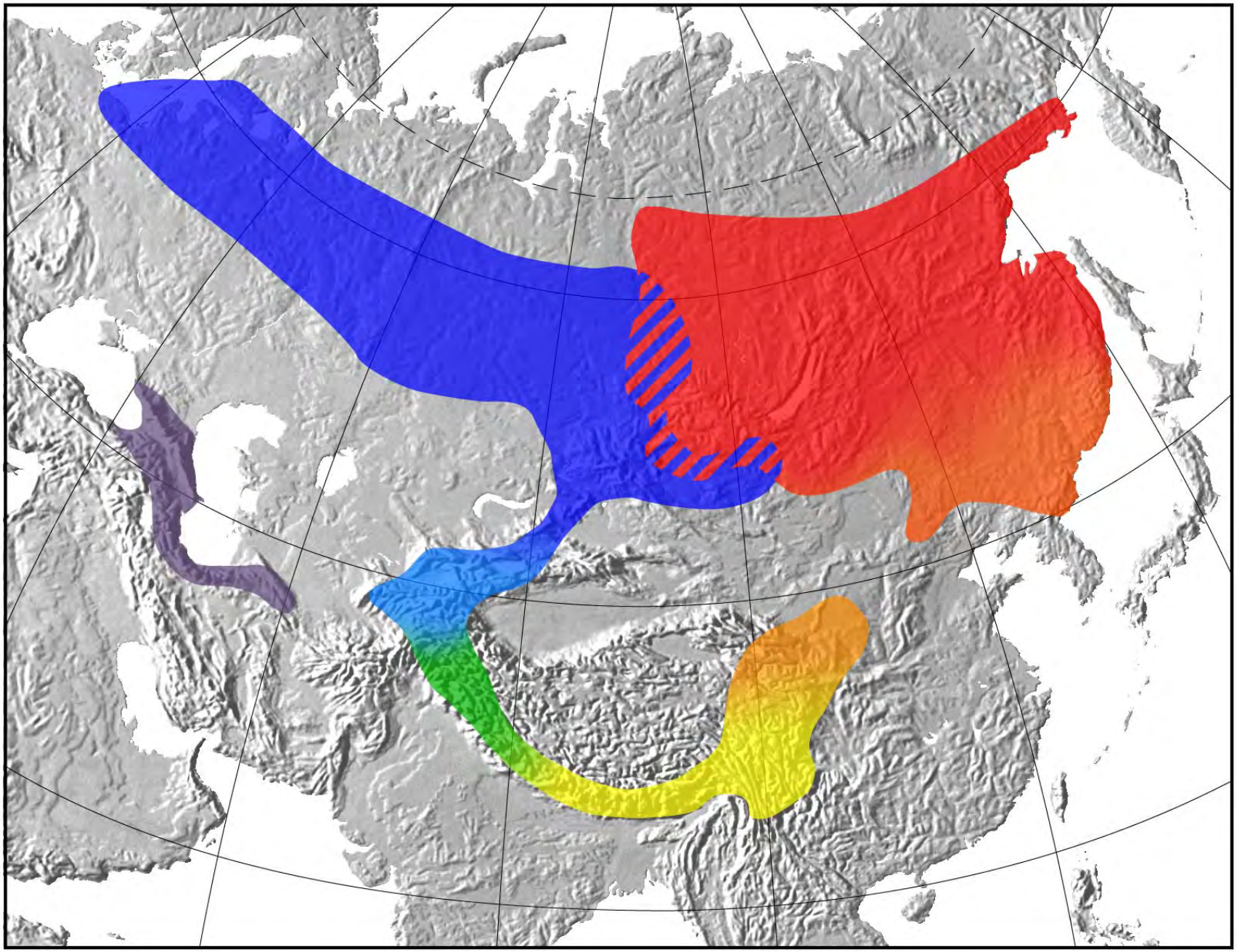






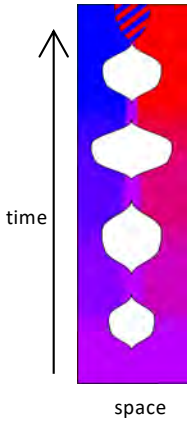






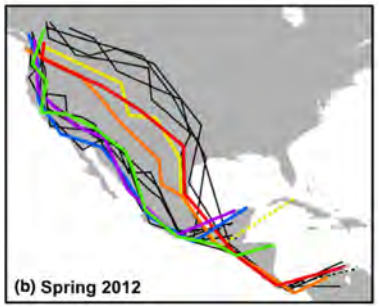
Now

Main points of the talk

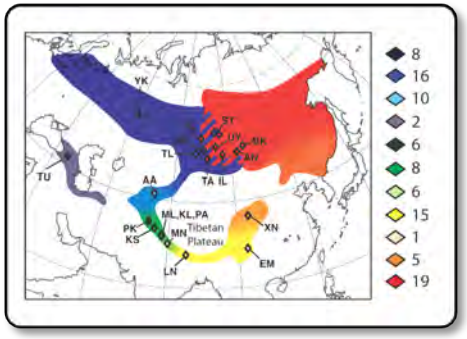


Speciation takes a long time, involving many cycles of hybridization

A bit of hybridization / gene flow can occur even after millions of years of divergence



Migratory route is genetically encoded, such that hybrids have intermediate (and likely inferior) routes.



Genomic patterns in the greenish warbler ring species suggest a complex history of geographic differentiation and hybridization / gene flow.

Acknowledgements (1)

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Field Museum

NSERC CRSNG

Environment Canada

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