

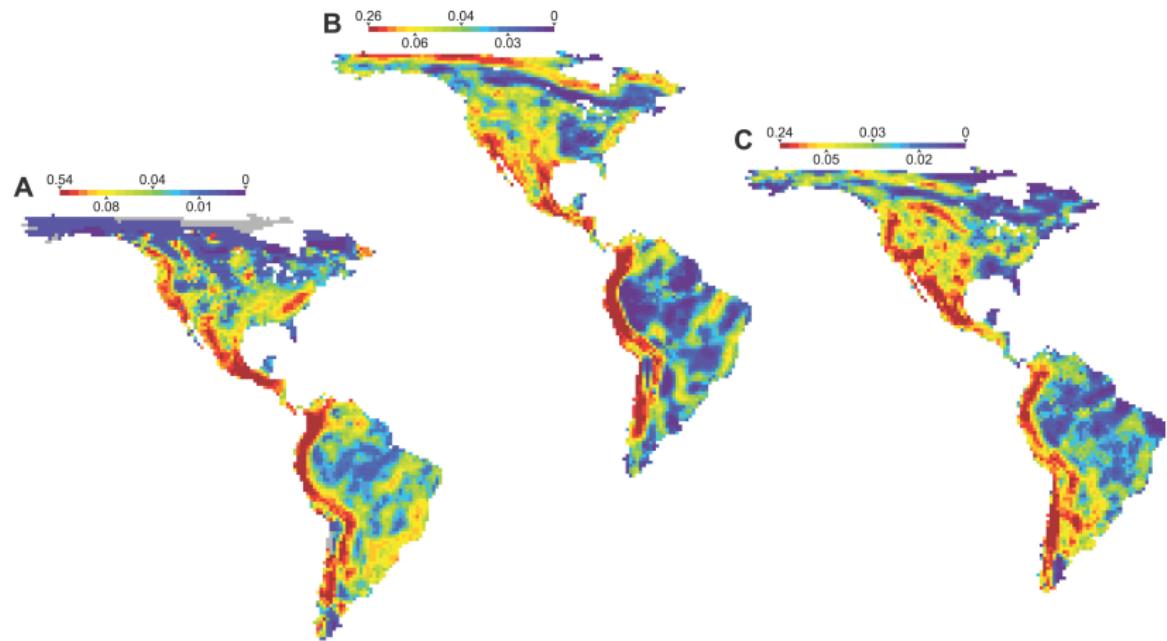


# Ecological and historical constraints on elevational ranges in birds

Ethan B. Linck

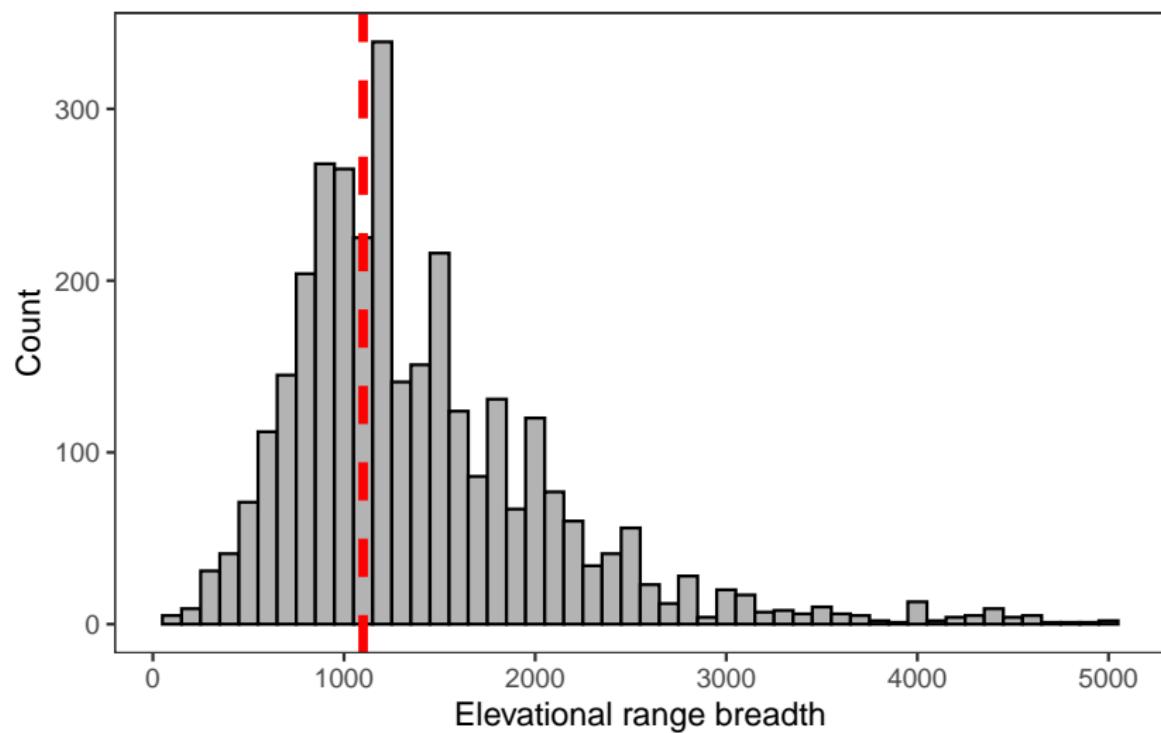
Montana State University  
Department of Ecology

# Big Pattern: $\beta$ diversity and elevation



(McKnight et al. 2007 *PLoS ONE*)

# Mountain biodiversity comes from elevational specialization



# Birds and biogeography



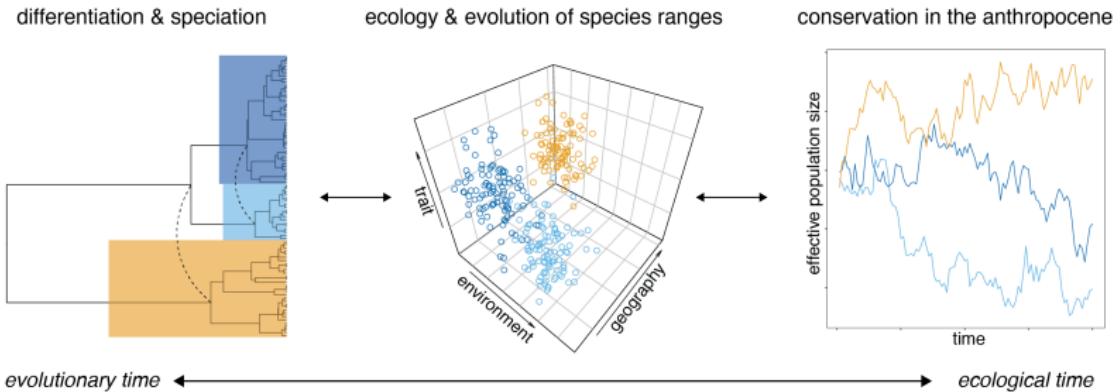
# Birds and biogeography



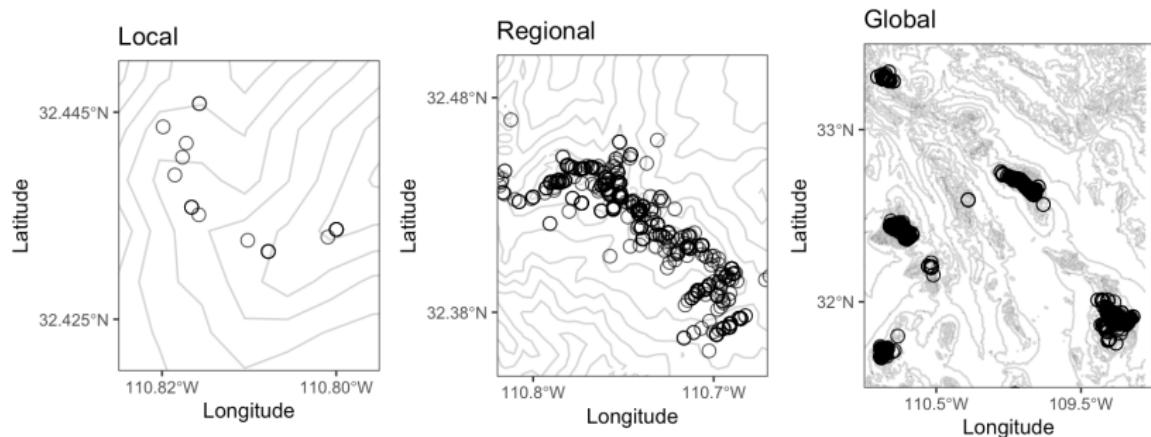
NEW BRITAIN THRUSH. JASON GRECC / MONTANA STATE UNIVERSITY

([https://www.montana.edu/ecology/msu\\_researchers\\_capture\\_photos\\_of\\_new\\_britain-thrush.html](https://www.montana.edu/ecology/msu_researchers_capture_photos_of_new_britain-thrush.html))

# Historical vs ecological biogeography



# Range limiting processes are scale dependent



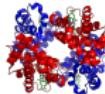
(Linck In Review *Am. Nat.*)

# Talk outline

- 1) How does plasticity in respiratory traits relate to range breadth?



- 2) Are molecular adaptations to high altitude predictable?



- 3) How does speciation generate  $\beta$  diversity across elevation?



1) How does plasticity in respiratory traits relate to range breadth?

## Acknowledgements:

- ▶ **Coauthors:** Jessie L. Williamson, Emil Bautista, Elizabeth J. Beckman, Phred M. Benham, Shane G. DuBay, L. Monica Flores, Chauncey R. Gadek, Andrew B. Johnson, Matthew R. Jones, Jano Núñez-Zapata, Alessandra Quiñonez, C. Jonathan Schmitt, Dora Susanibar, Jorge Tiravanti C., Karen Verde-Guerra, Natalie A. Wright, Thomas Valqui, Jay F. Storz, Christopher C. Witt
- ▶ **Funding:** NSF DBI #1907353, DEB #1146491, and DEB #0543556

# Distributions on environmental gradients

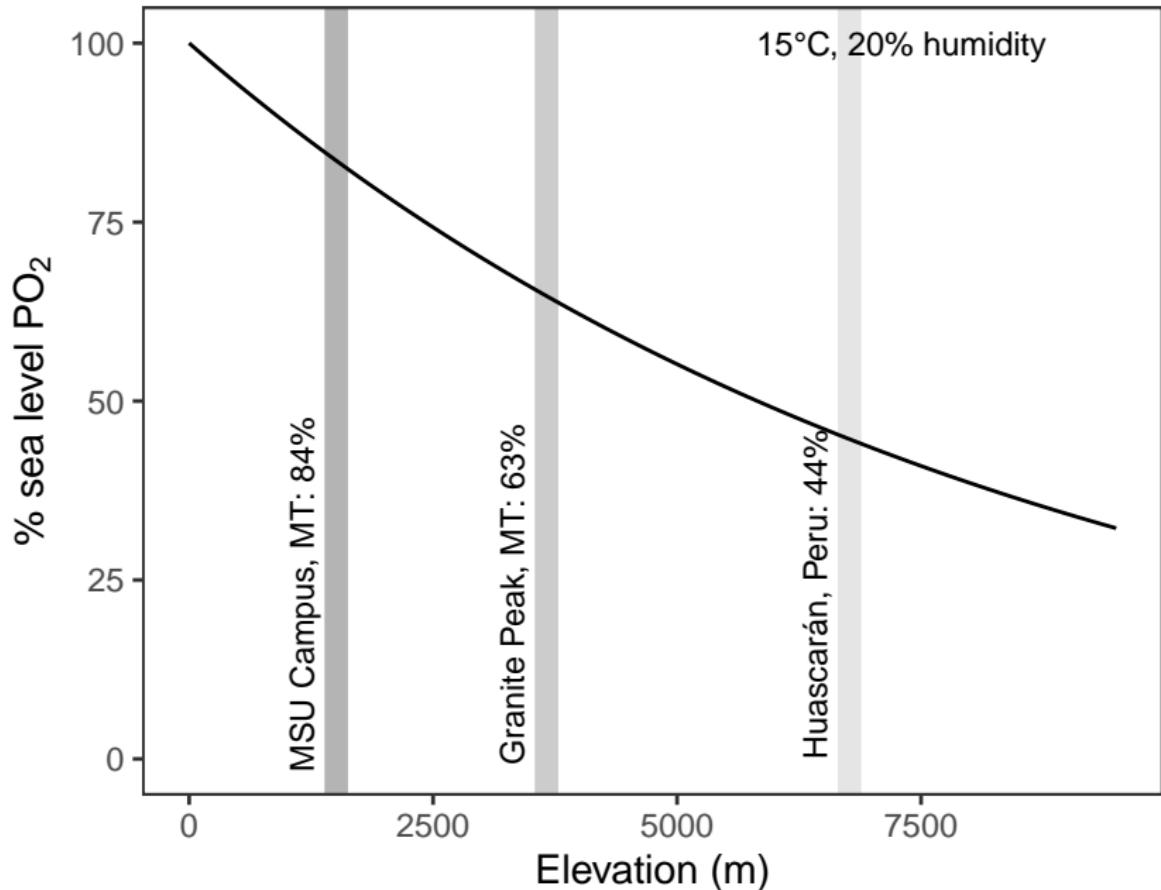
"In their simplest form the models state that the occurrence of species is limited respectively by: (i) physical or biological conditions that vary in parallel with the measured gradient, (ii) competitive exclusion and (iii) environmental discontinuities (ecotones). . ." (Terborgh 1971 *Ecol.*)



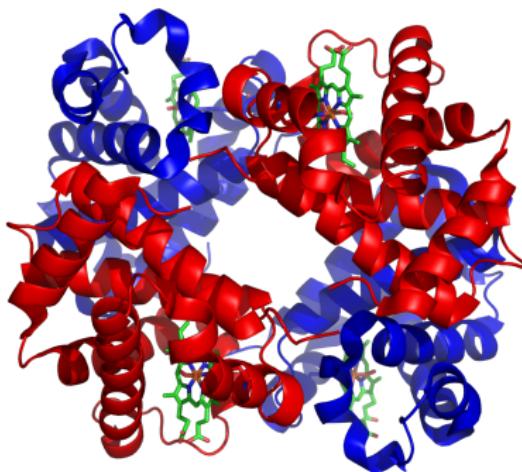
# Humid tropical elevational gradients lack ecotones



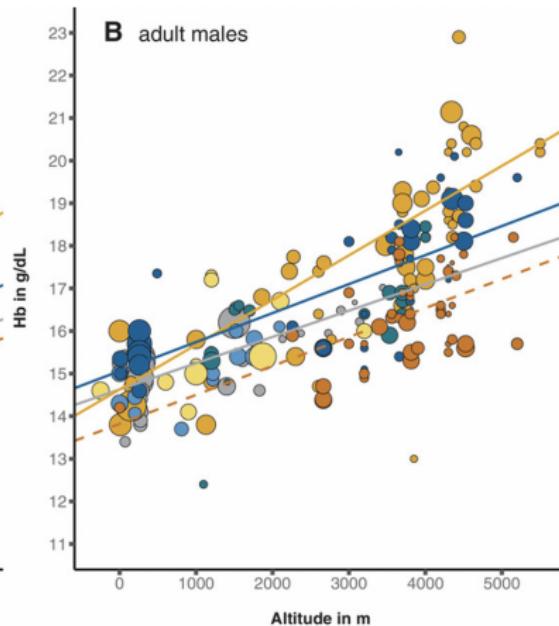
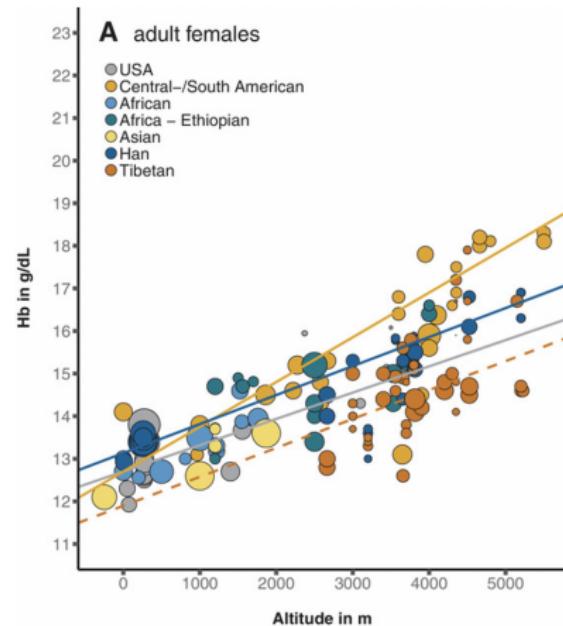
# $PO_2$ varies in parallel with elevation



Hemoglobin facilitates oxygen transport for aerobic respiration

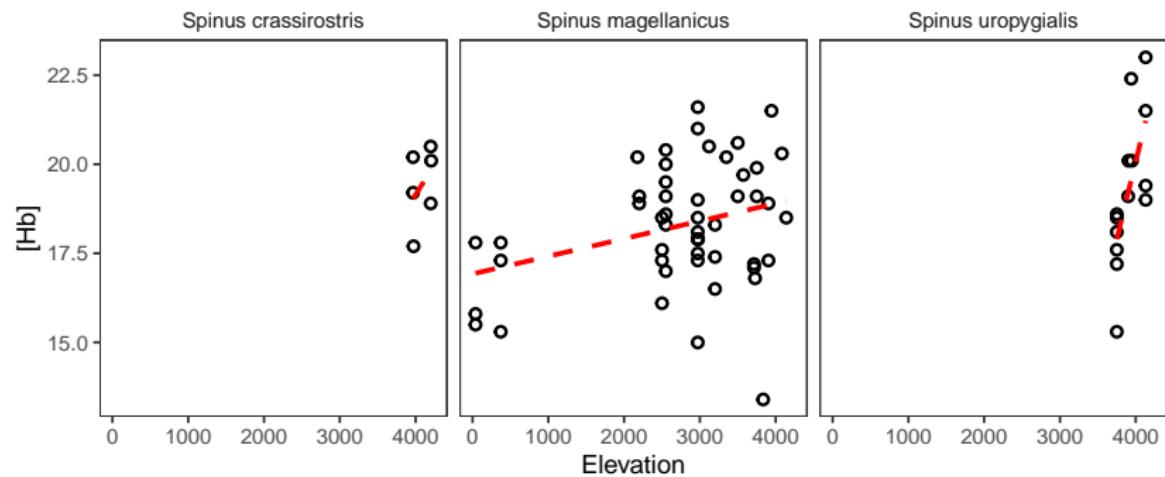


# The increase in [Hb] with altitude varies among human populations

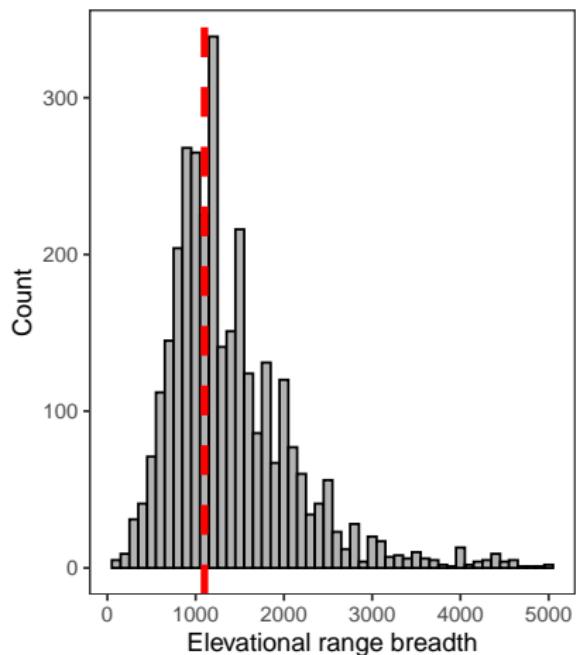
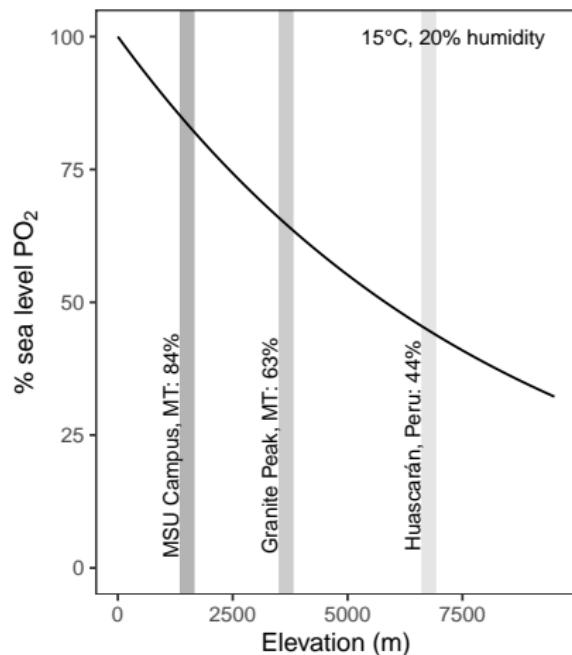


(Gassmann et al. 2019)

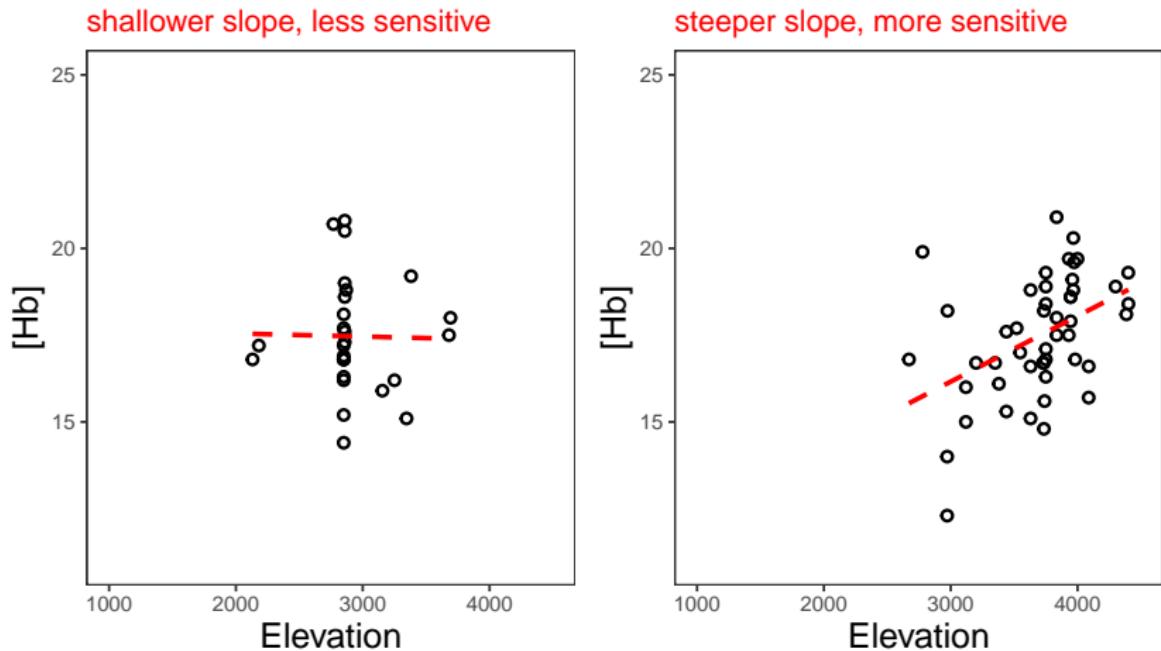
# The increase in [Hb] concentration with altitude varies among Andean bird species



# Does blood- $O_2$ carrying-capacity influence elevational specialization?



# Metric: Respiratory “plasticity” ( $[Hb]$ sensitivity)

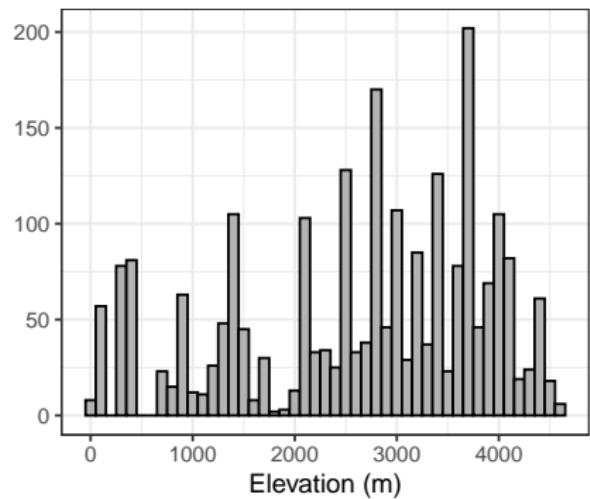
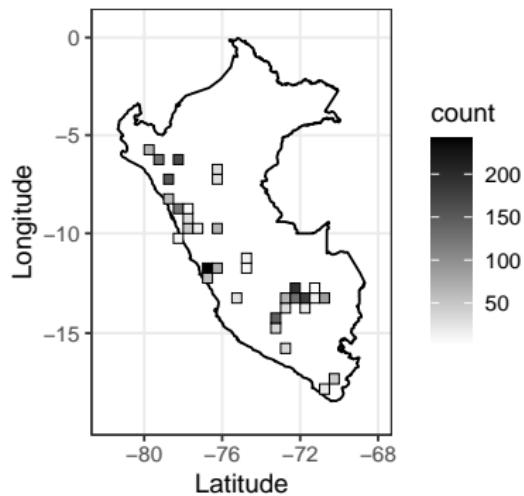


$H_1$ : Respiratory plasticity influences niche breadth

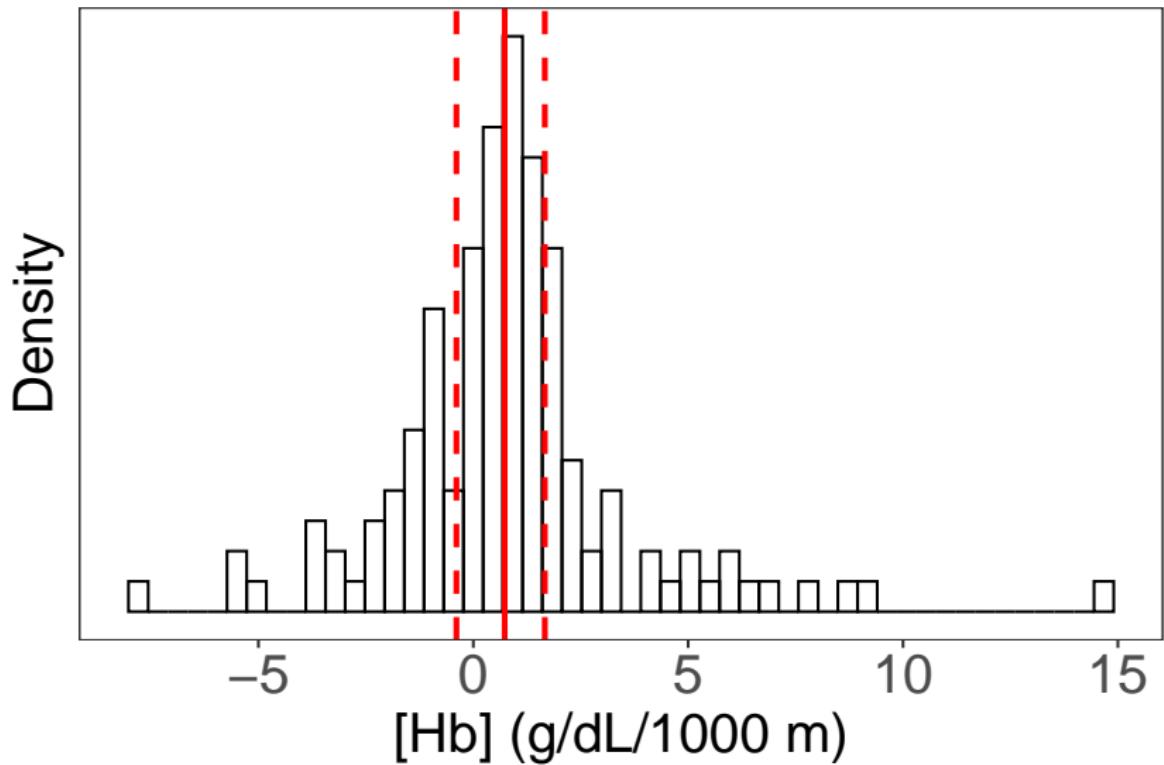


# Methods

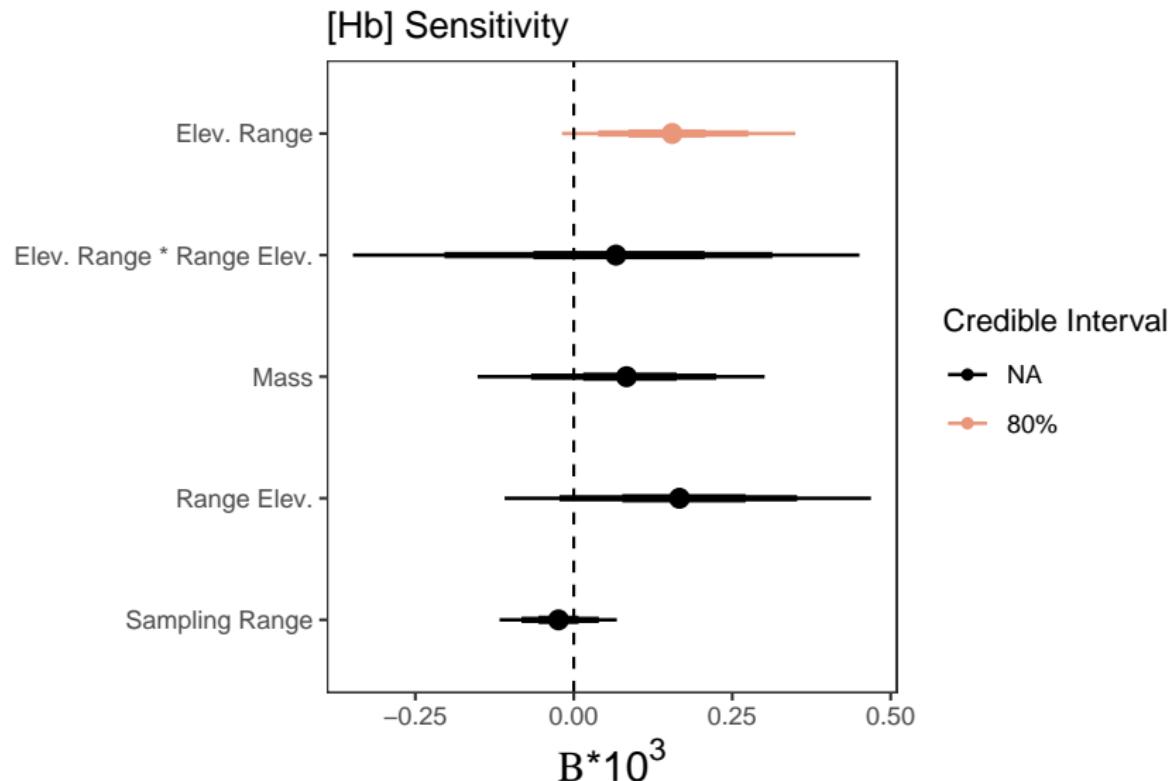
- ▶ [Hb] (+ other traits) from 2367 individuals, 136 species
- ▶ Bayesian linear models



## Respiratory plasticity varies but mostly positive



# $H_1$ : Elevational generalists have greater respiratory plasticity



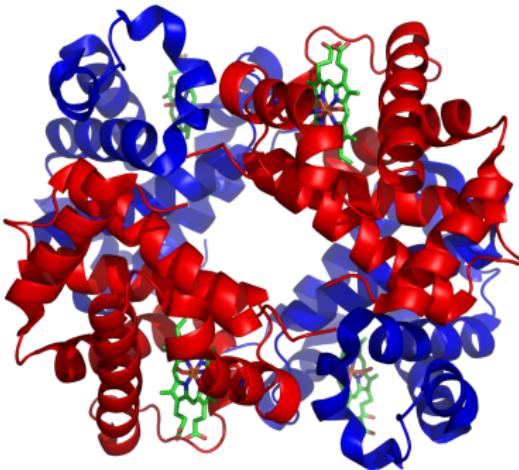
We suggest: Respiratory plasticity can facilitate elevational range expansion

2) Are molecular adaptations to high altitude predictable?

## Acknowledgements:

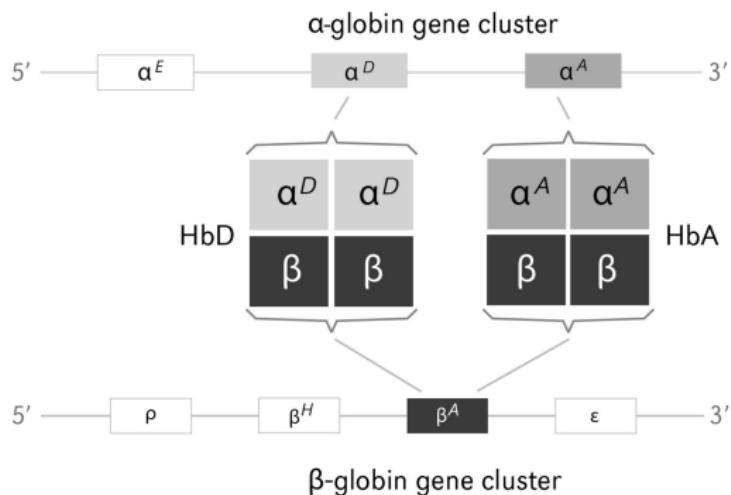
- ▶ **Coauthors:** Libby Beckman, Andrea Chavez, Chauncey Gadek, Jenna McCullough, Chandru Natarajan, Jay Storz, Christopher C. Witt
- ▶ **Funding:** NSF DBI #1907353, DEB #1146491, and DEB #0543556

# Hemoglobin structure impacts oxygen transport



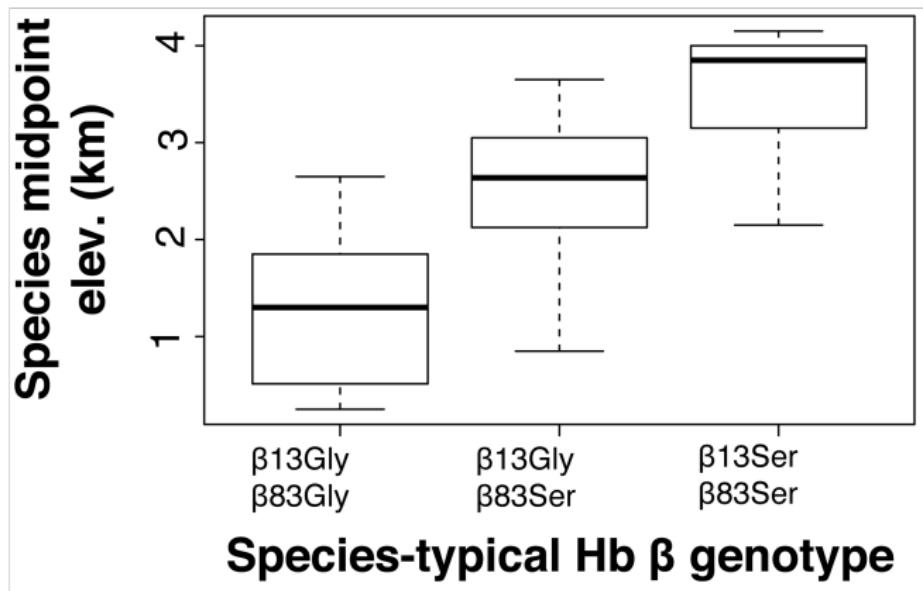
red= $\alpha$ -globin subunit, blue= $\beta$ -globin subunit,  
green=iron-containing hemes

# Three genes code for adult avian hemoglobin isoforms



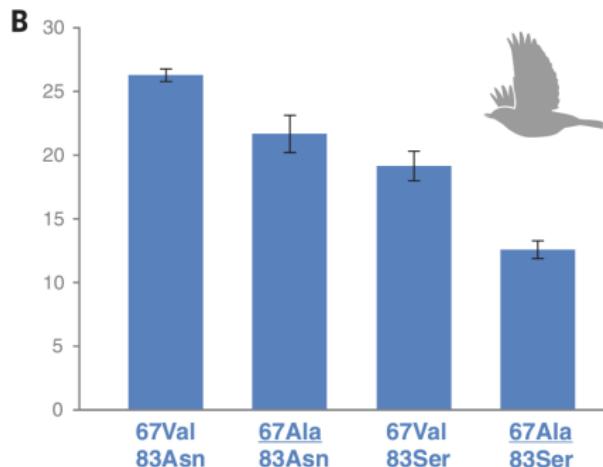
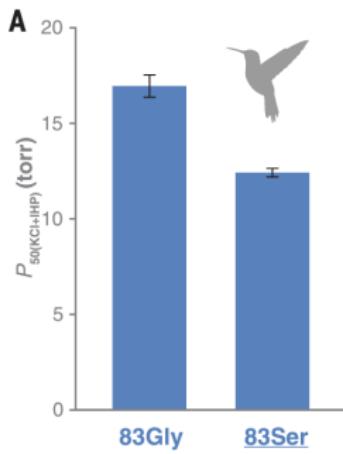
(Opazo et al. 2015 *Mol. Biol. Evol.*)

# $\beta$ -Ser substitutions associated with elevation in hummingbirds



(Projecto-Garcia et al. 2013 PNAS)

# $\beta$ -Ser increases oxygen carrying capacity in hummingbirds and diglossine tanagers



(Natarajan et al. 2016 *Science*)

# Diglossine tanagers



*Conirostrum*



*Diglossa*



*Diuca*



*Catamenia*

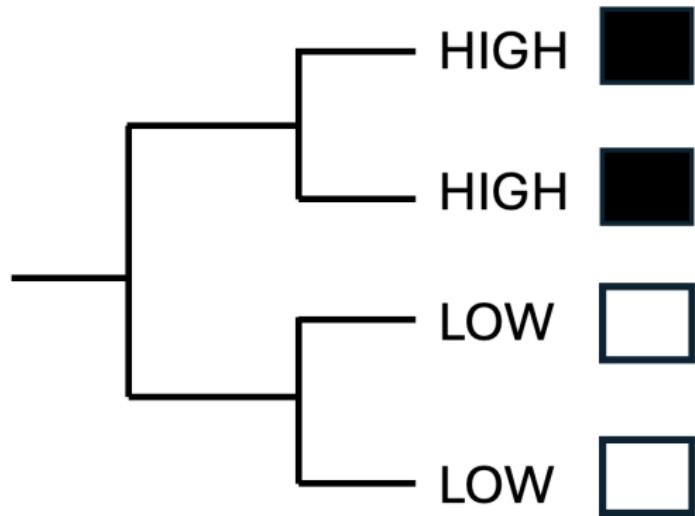


*Sicalis*



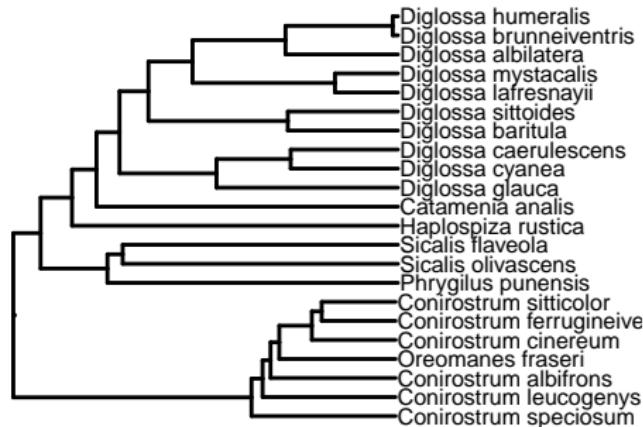
*Xenodacnis*

*H*<sub>1</sub>: Functional substitutions to Hb are predictably associated with elevation in Diglossines, too

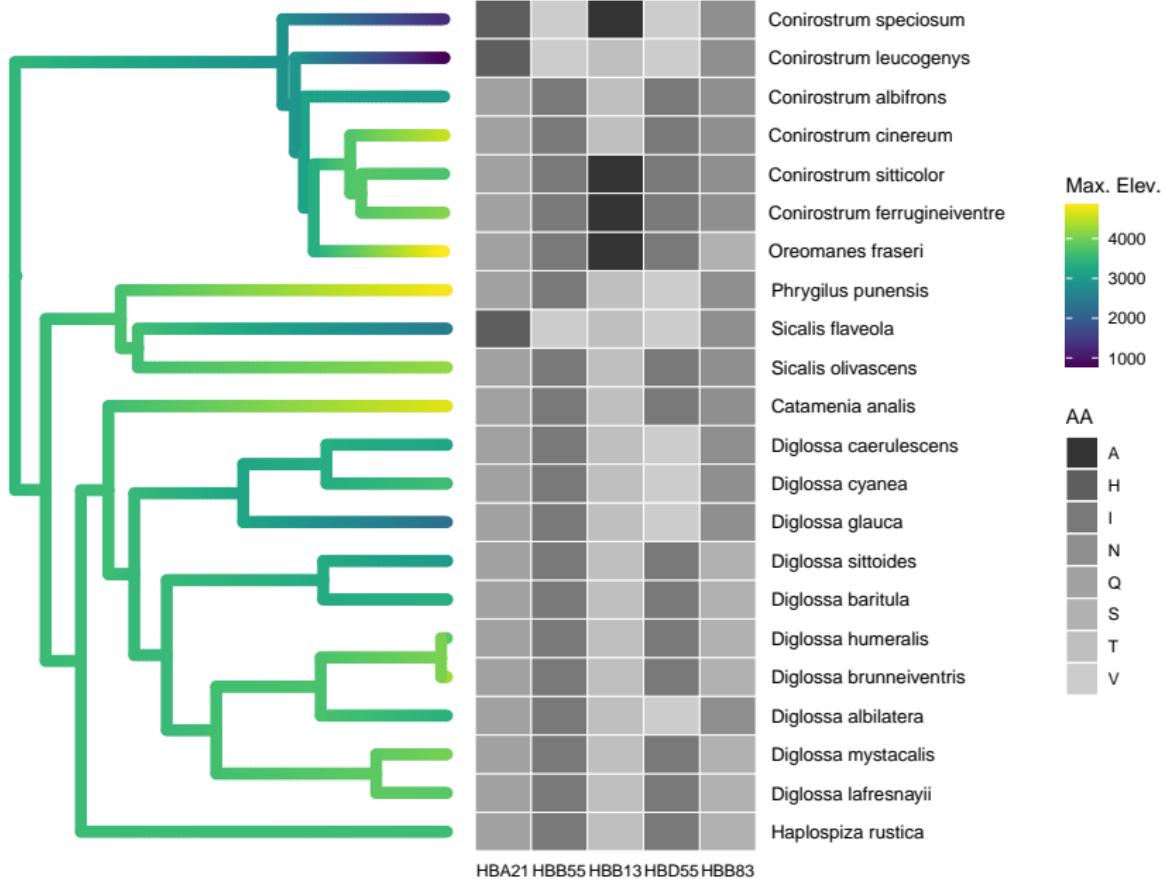


# Methods

- ▶ Sequence capture of all 7 **Hb** genes for 88 individuals of 22 species
- ▶ CDS annotation and amino acid substitution
- ▶ Ancestral state reconstruction
- ▶ Phylogenetic linear mixed models with Brownian motion trait evolution



# Repeated Hb substitutions (but not $\beta$ -83Ser)



We conclude: evolution is both predictable and contingent (total cop out, lol)

3) How does speciation generate  $\beta$  diversity across elevation?

## Acknowledgements:

- ▶ **Collaborators and Coauthors:** Salape Tulai, Bulisa Iova, Georgia Kapui, Ben Freeman, Jack Dumbacher, John Klicka, C.J. Battey, Kevin Epperly
- ▶ **Funding:** NSF DDIG #1701224, NSF DEB #0108247, and NDSEG and WRF-Hall Fellowships

# Elevational replacements

FEATURES OF THE EASTERN HIGHLANDS

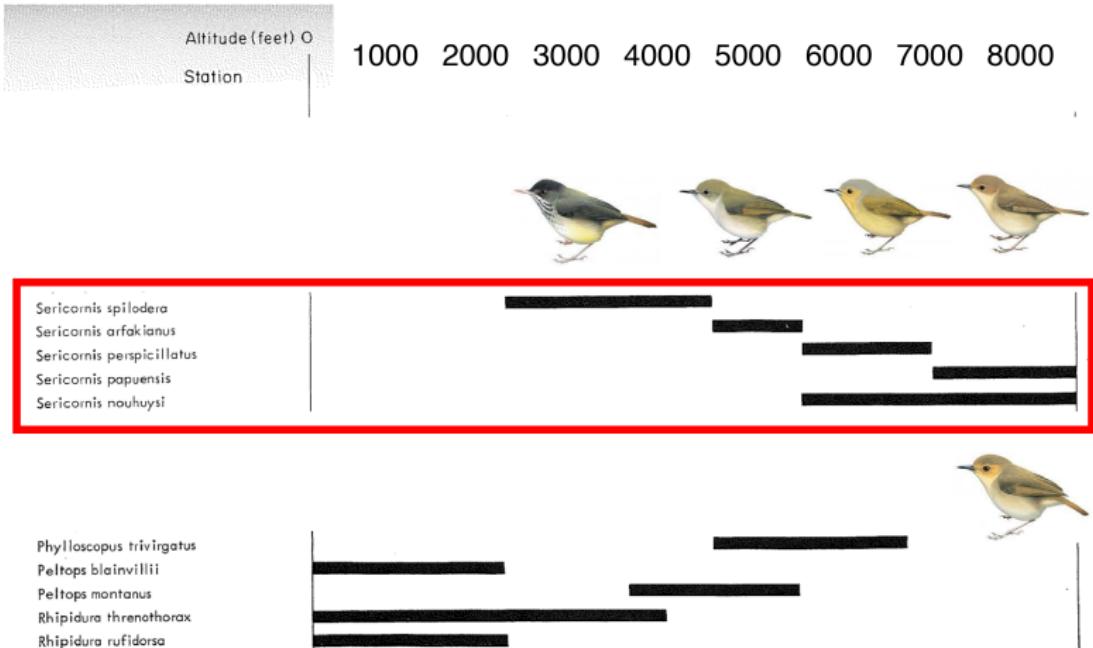
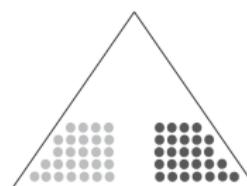
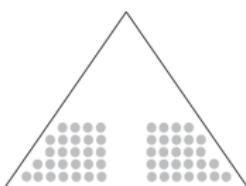
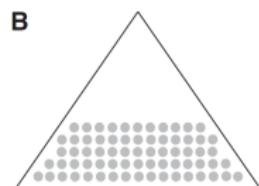
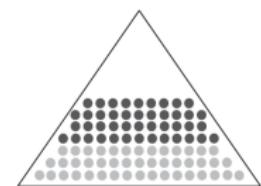
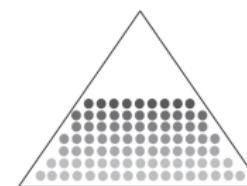
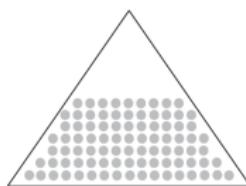
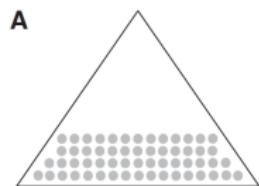


FIG. 4 (cont.). Altitudinal ranges of 166 species in the Karimui area.

(Diamond 1972)

# Alternate paths to the same result



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common ancestor

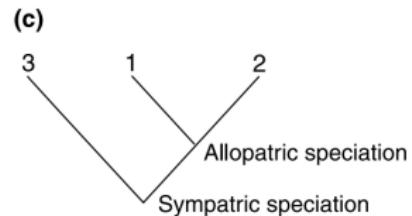
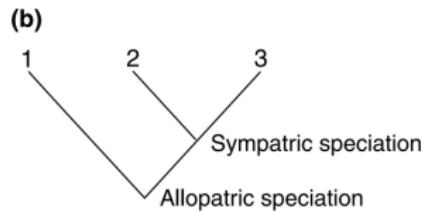
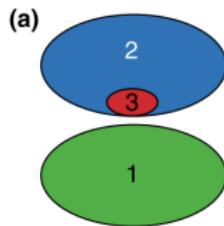
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intermediate divergence

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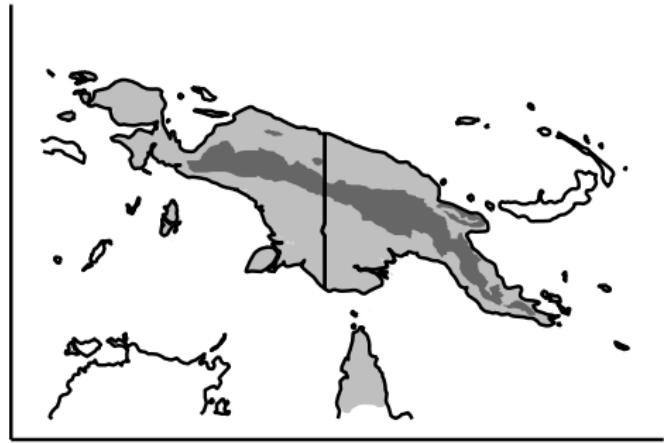
speciation

# Phylogeny and the geography of speciation



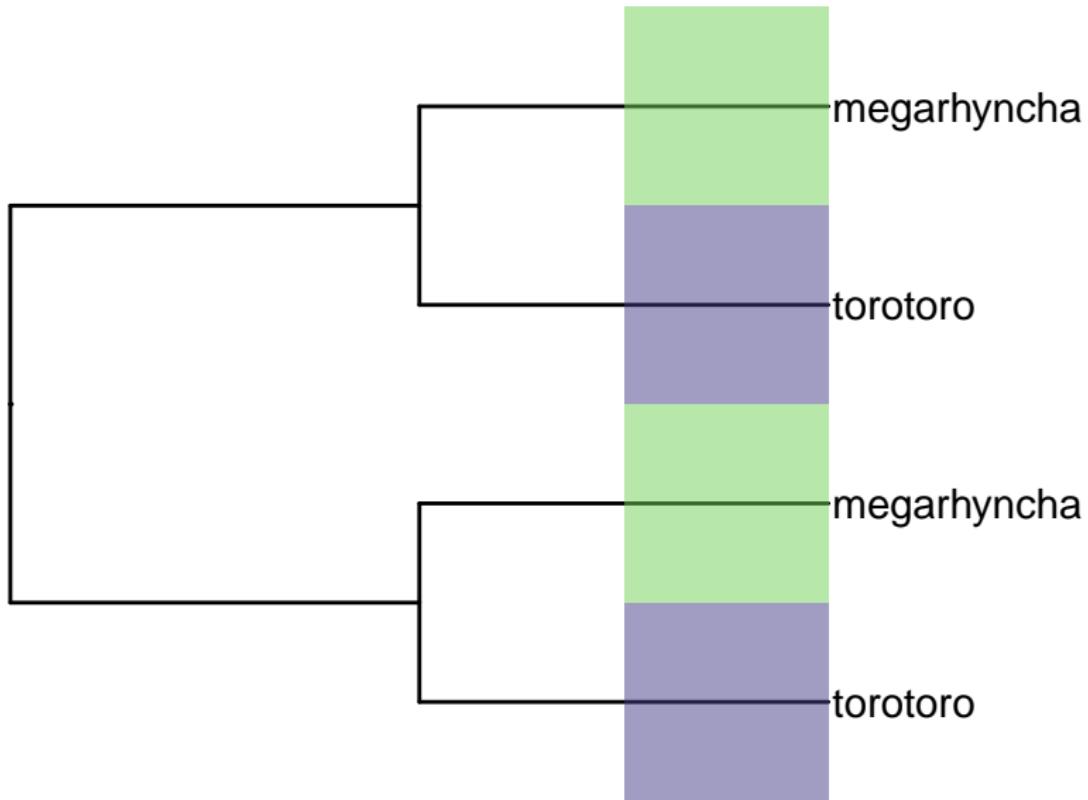
(Losos & Glor 2003)

# *Syma* kingfishers as natural experiment

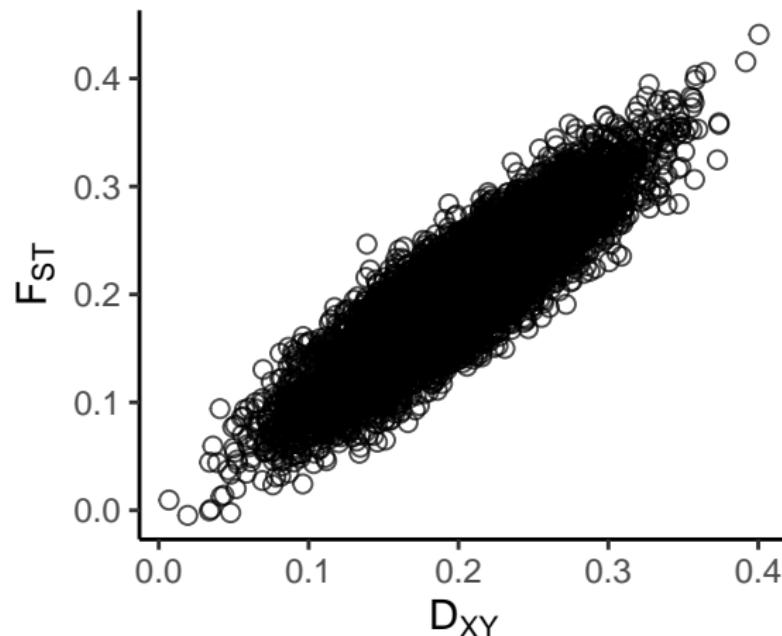


(art by Kevin Epperly)

# $H_1$ : Parallel parapatric (ecological) speciation



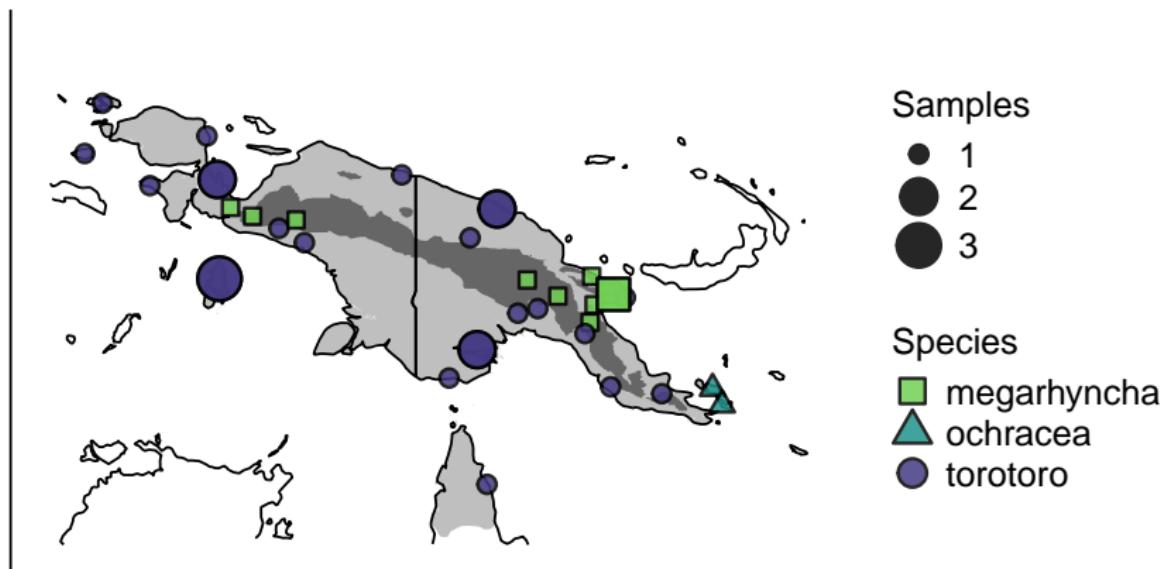
# $H_1$ : Parallel parapatric (ecological) speciation



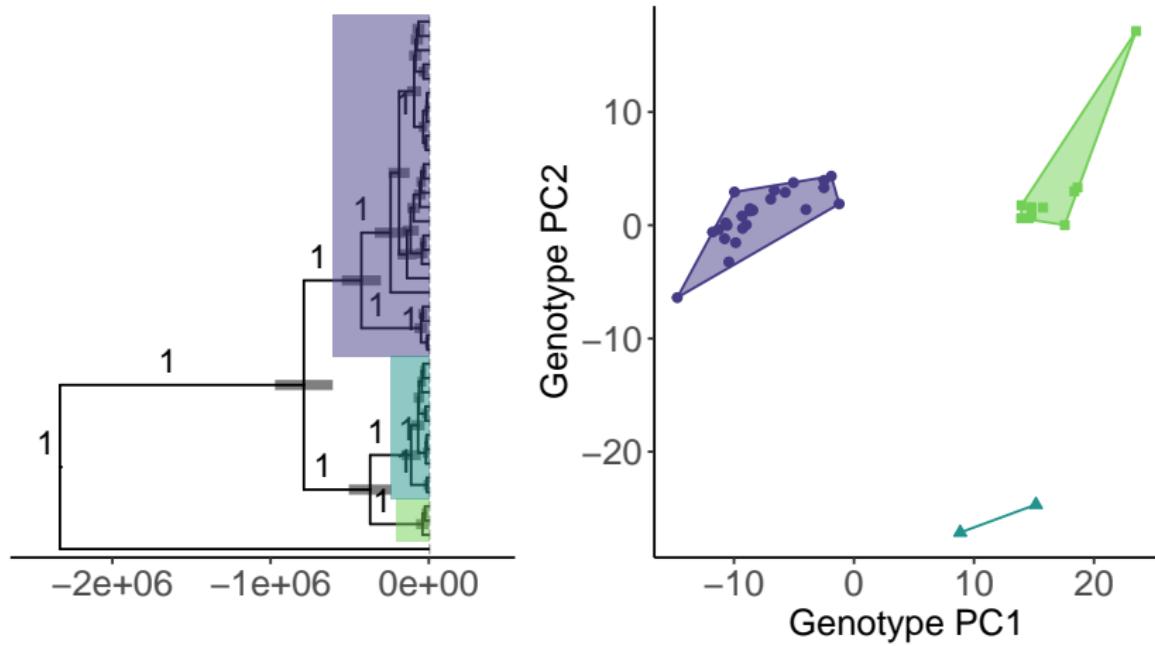
$$F_{ST} = \frac{\pi_{\text{Between}} - \pi_{\text{Within}}}{\pi_{\text{Between}}}; \quad D_{XY} = \sum_{ij} x_i y_j d_{ij}$$

# Methods

- ▶ mtDNA and nuclear DNA from fresh and historic tissues
- ▶ phylogenetic inference, clustering, and demographic modeling

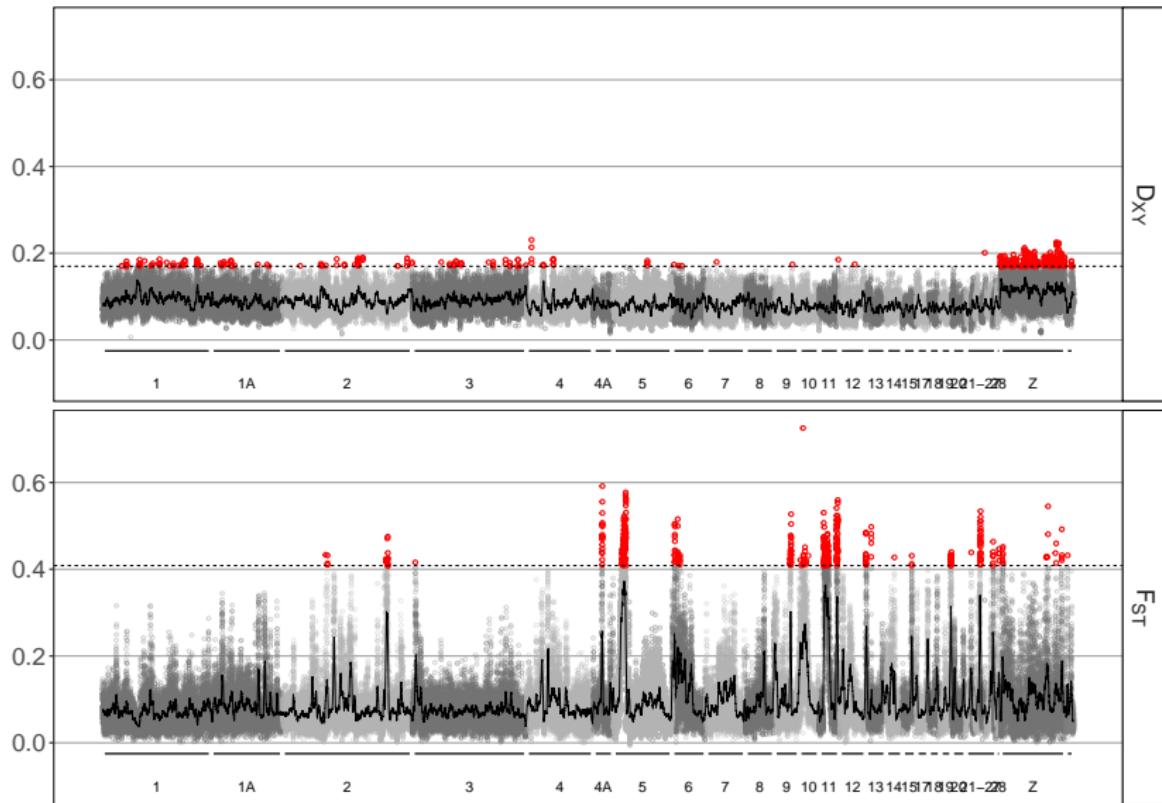


# No evidence for parallel parapatric speciation

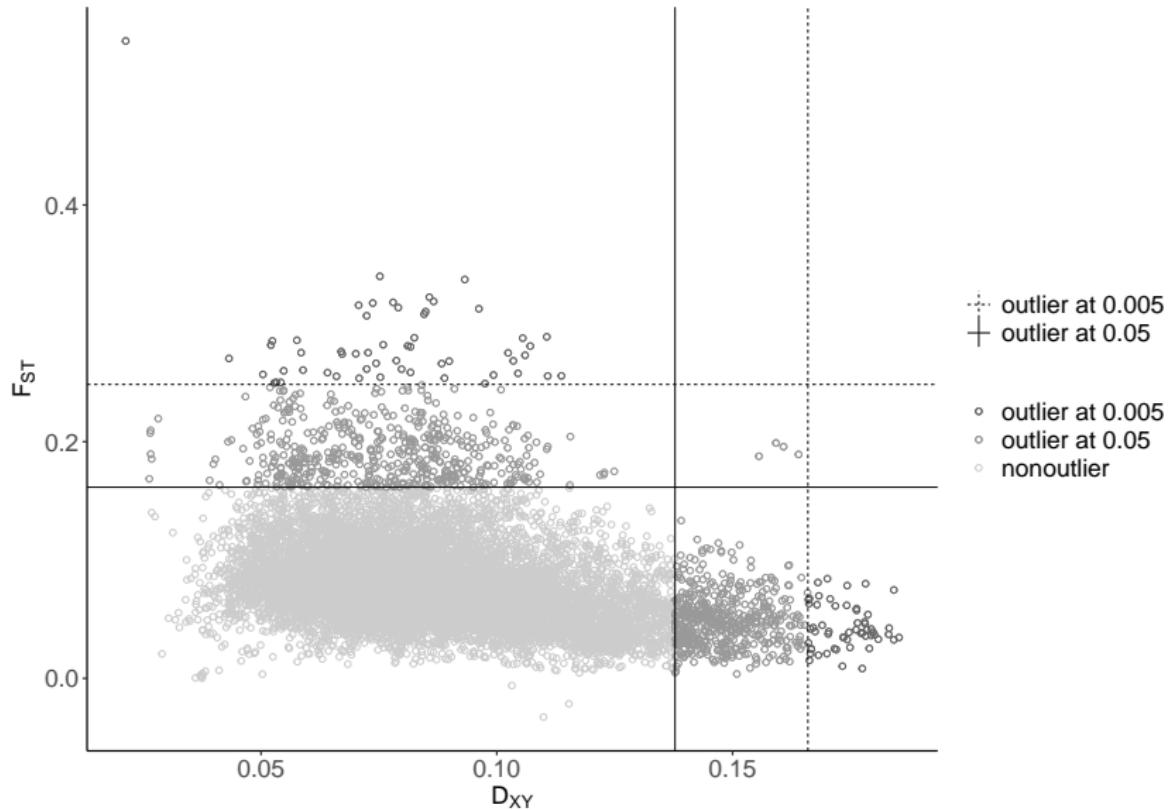


(Linck et al. 2020 *J. Evol. Biol.*)

# Heterogeneous divergence across the genome

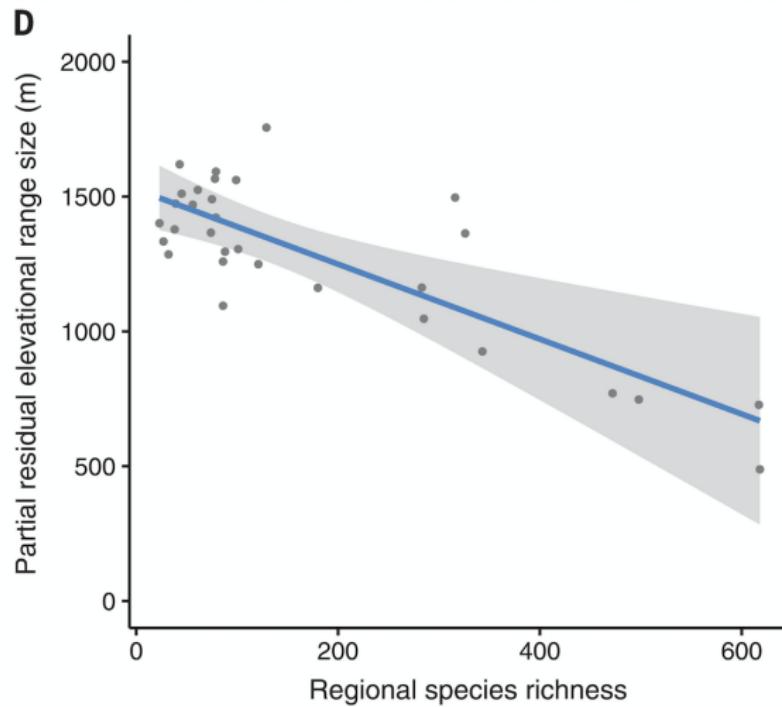


# Absolute and relative divergence not correlated



We conclude: speciation in allopatry is more likely (but parapatric speciation is possible, and gene flow was involved)

# The specter of other variables



## Why this is all a little unsatisfying (or motivating?)

“However if many causes contribute to an observed pattern, none will be eliminated from consideration by a properly designed experiment... The objective of investigation in cases of this sort is not to determine the single cause of a pattern, as no such cause exists, but rather to assign relative importances to the contributions of, and interactions between, a number of processes, all known or reasonably suspected of operating to some degree” (Quinn & Dunham 1983 *Am. Nat.*)

# Resources

- ▶ slides and code: <https://github.com/elinck/misctalks>
- ▶ website: <https://elinck.org/>
- ▶ twitter: @ethanblinck

## References

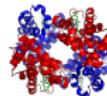
- ▶ McKnight et al. 2007. *PLoS Biology*, 5(10), e272.
- ▶ Terborgh 1971. *Ecology*, 52(1), 23-40.
- ▶ Linck et al. 2023. *Am. Nat.* 201(5), 741-754.
- ▶ Gassmann et al. 2019. *Annals of the New York Academy of Sciences*, 1450(1), 204-220.
- ▶ Projecto-Garcia et al. 2013. *PNAS*, 110(51), 20669-20674.
- ▶ Natarajan et al. 2016. *Science*, 354(6310), 336-339.
- ▶ Diamond 1972. *Avifauna of the Eastern Highlands of New Guinea*.
- ▶ Linck et al. 2020. *J. Evol. Biol.*, 33(11), 1643-1652.
- ▶ Losos & Glor 2003. *TREE*, 18(5), 220-227.
- ▶ Freeman et al. 2022. *Science*, 377(6604), 416-420.
- ▶ Quinn & Dunham 1983. *The American Naturalist*, 122(5), 602-617.

# Thanks!

- 1) [Hb] sensitivity is correlated with range breadth



- 2) Adaptive Hb evolution is predictable but context dependent



- 3) Parapatric speciation is unlikely, but elevational gradients help maintain species limits

