

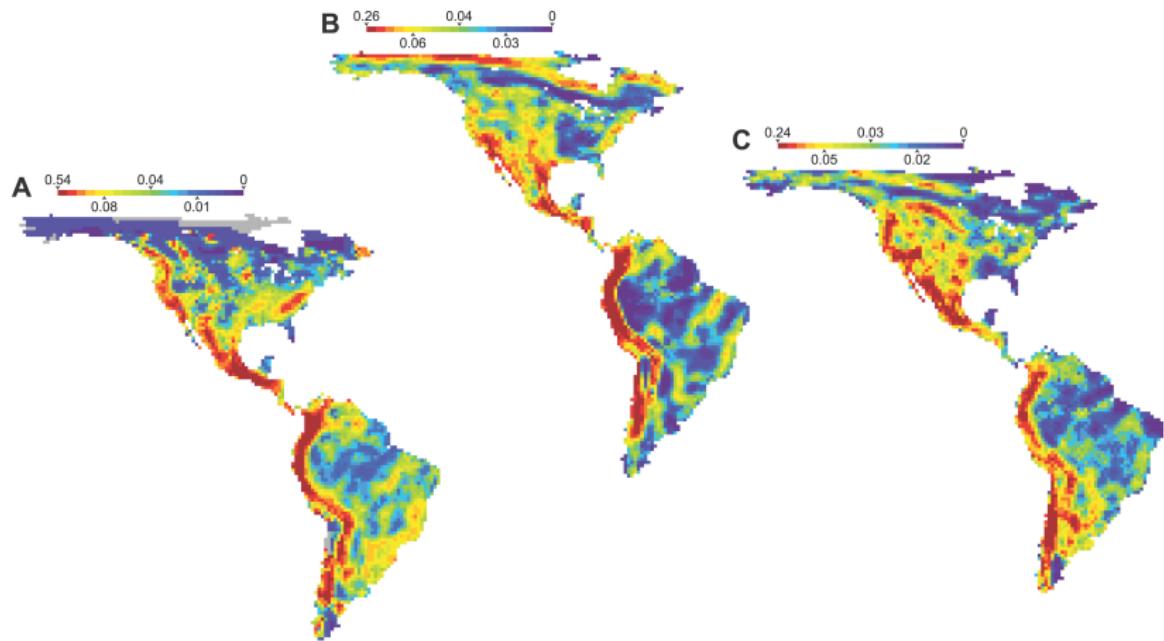


# The evolution of elevational specialization (and why studying it is hard)

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# Big Pattern: $\beta$ diversity and elevation



(McKnight et al. 2007)

# Elevational specialization



(Freeman & Montgomery 2015)

# Big Questions

- ▶ What are the evolutionary *causes* of elevational specialization?
- ▶ What are its possible *consequences*?
- ▶ (Why is this such a hard question to study?)

Littler Question 1: Does parapatric speciation generate  $\beta$  diversity?

## 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

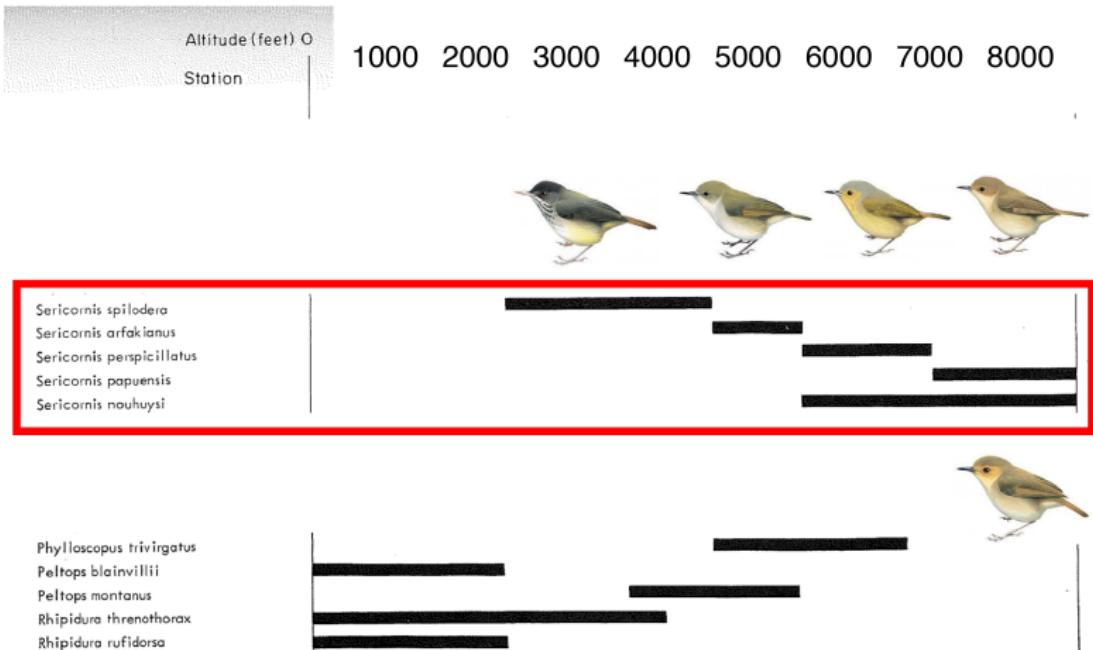
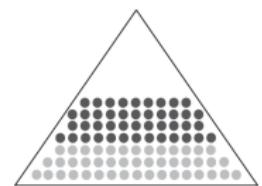
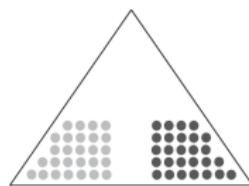
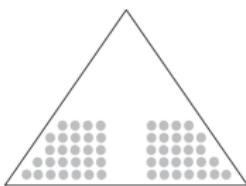
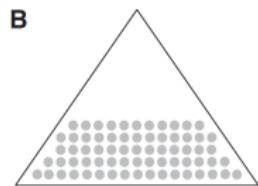
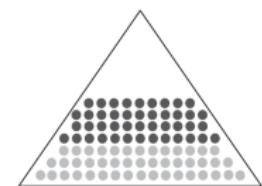
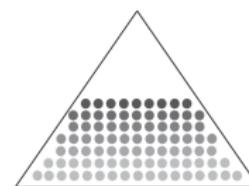
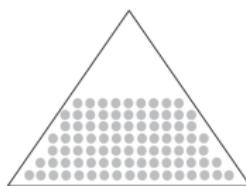
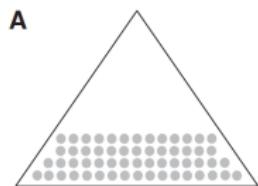


FIG. 4 (cont.). Altitudinal ranges of 166 species in the Karimui area.

(Diamond 1972)

# Alternate paths to the same result



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common ancestor

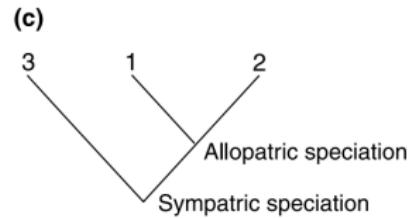
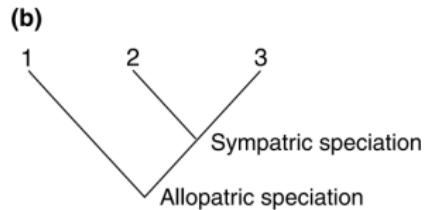
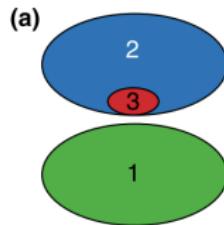
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intermediate divergence

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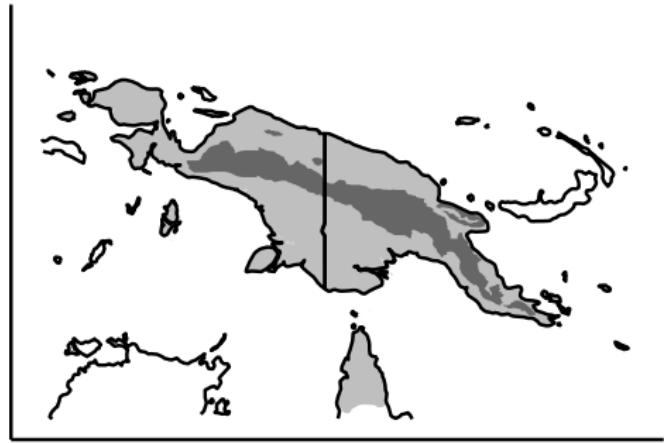
speciation

# Phylogeny and the geography of speciation



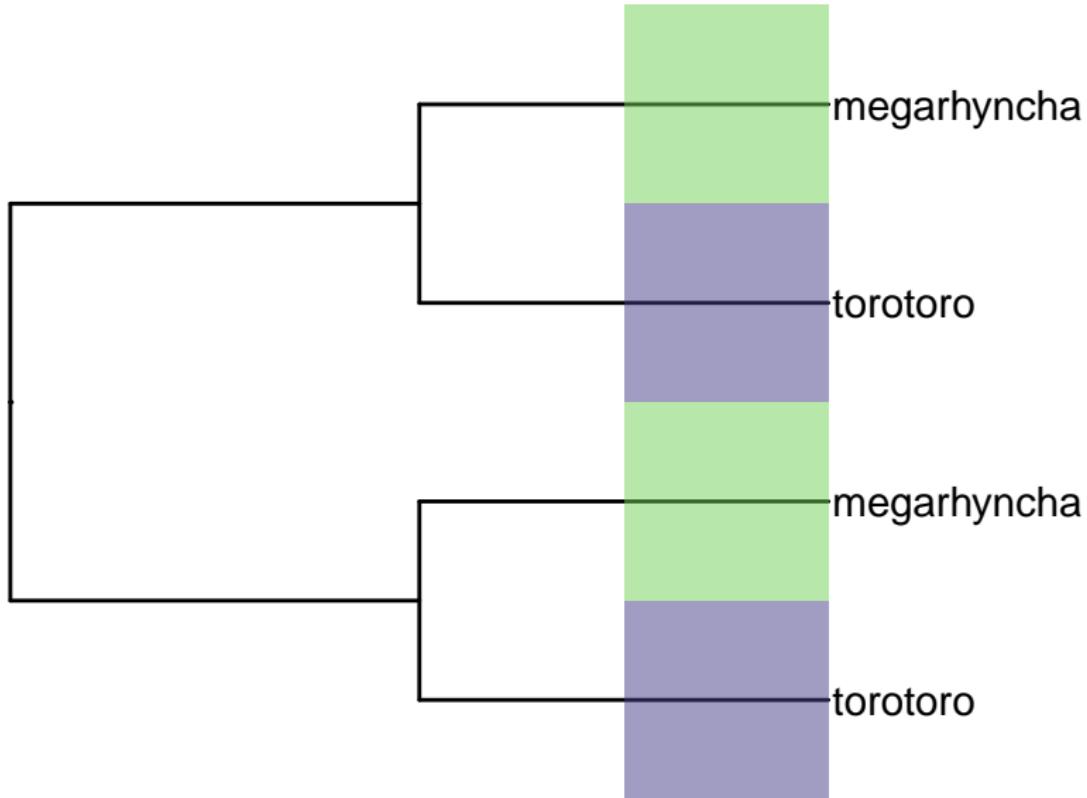
(Losos & Glor 2003)

# *Syma* kingfishers as natural experiment



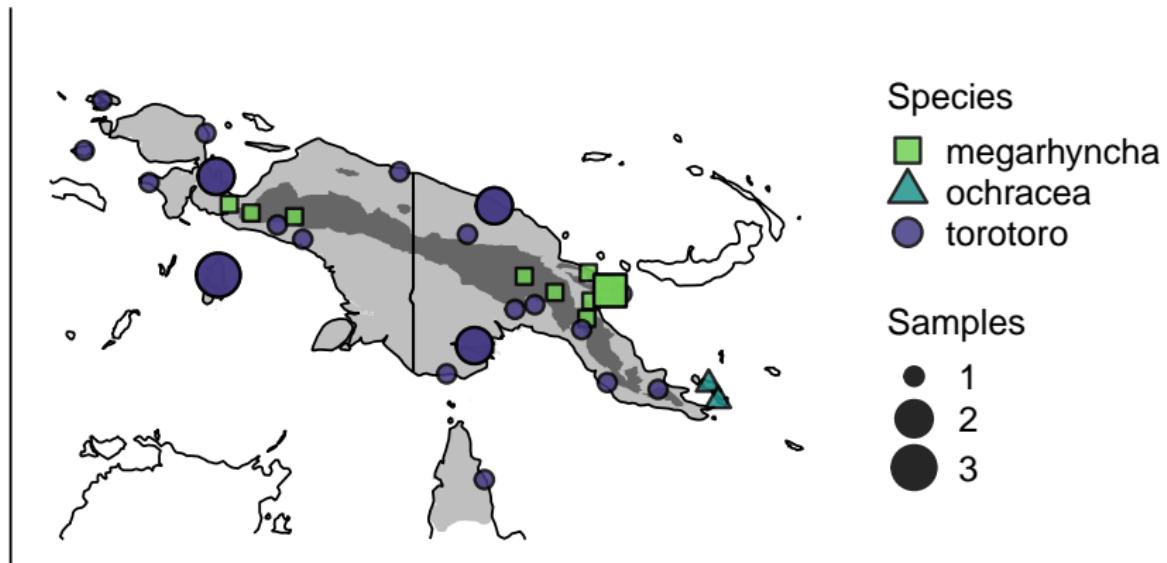
(art by Kevin Epperly)

# $H_1$ : Parallel parapatric speciation

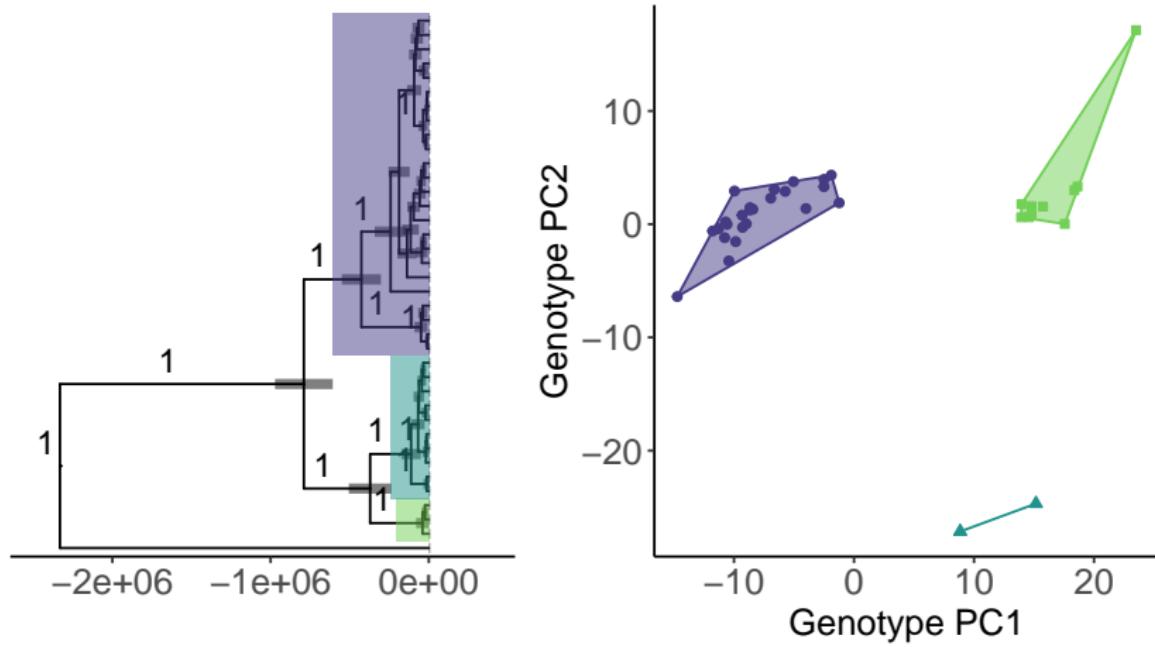


# Methods

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



# No evidence for parallel parapatric speciation



(Linck, Freeman, & Dumbacher 2020)

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

## Why it's unsatisfying:

"Formal hypotheses generally cannot usefully be posed in a way that allows meaningful disproof of a finite number of discrete possibilities" (Quinn & Dunham 1983, "On Hypothesis Testing in Ecology and Evolution", *The American Naturalist*)

## Why it's unsatisfying, part 2:

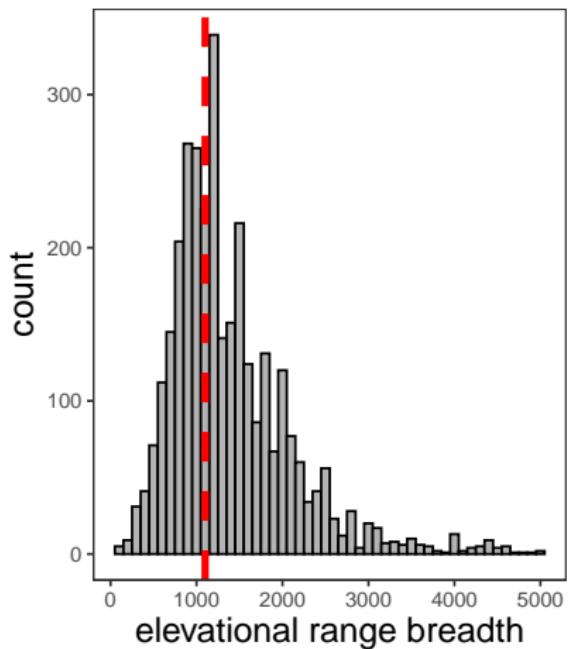
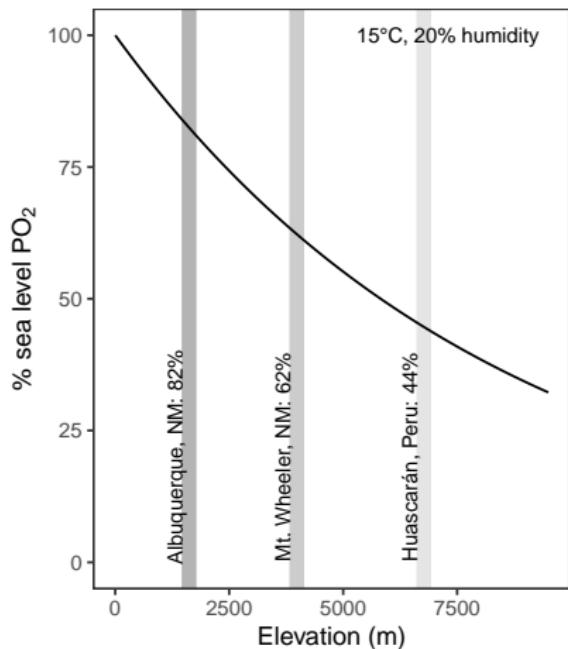
"Physicists and chemists often have genuine difficulty in understanding the biologist's stress of the unique... individuality [is] so characteristic of the organic world, where all individuals are unique; all stages in the life cycle are unique; all populations are unique; all species and higher categories are unique; all interindividual contacts are unique; all natural associations of species are unique; and all evolutionary events are unique"  
(Mayr 1961, "Cause and Effect in Biology", *Science*)

Littler Question 2: Does physiology limit elevational ranges?

## Acknowledgements:

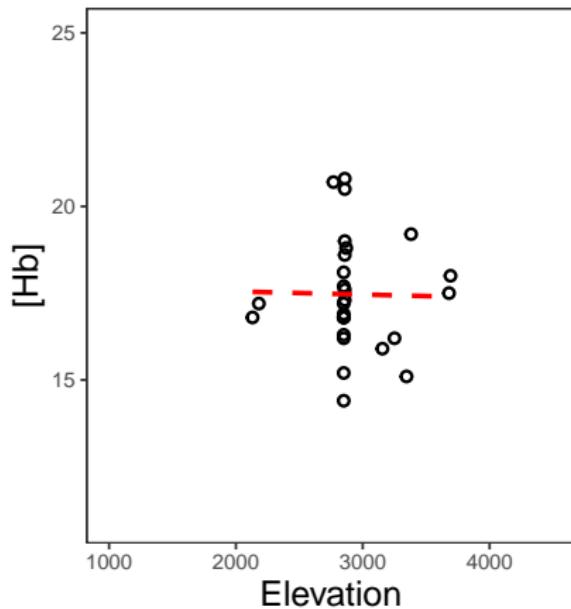
- ▶ **Collaborators and Coauthors:** Jessie L. Williamson, Emil Bautista, Elizabeth J. Beckman, Phred M. Benham, Shane G. DuBay, L. Monica Flores, Chauncey R. Gadek, Andrew B. Johnson, Matthew R. Jones, Jano Núñez-Zapata, Alessandra Quiñonez, C. Jonathan Schmitt, Dora Susanibar, Jorge Tiravanti C., Karen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

# Blood $O_2$ -carrying capacity and elevational specialization

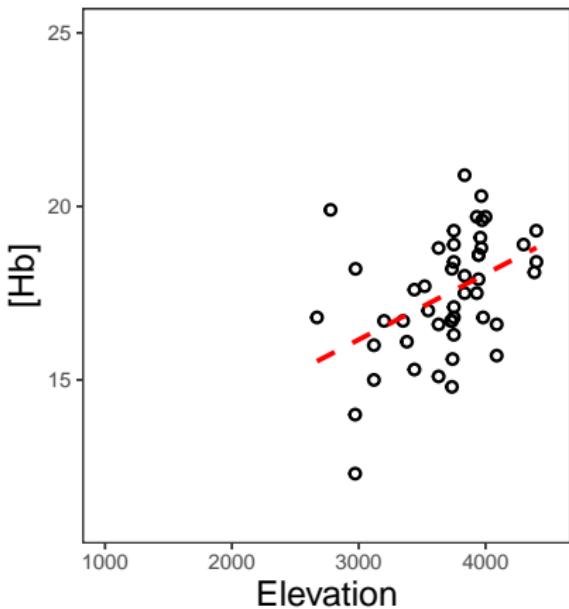


# Respiratory plasticity

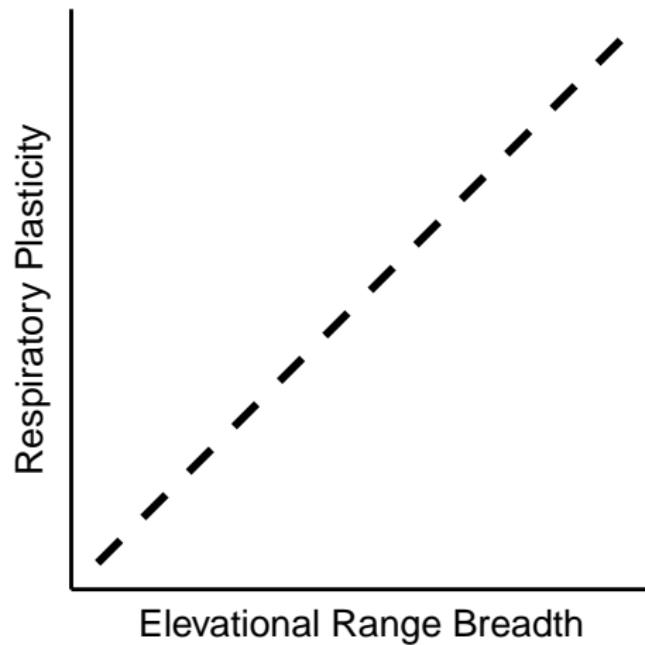
shallower slope, less plastic



steeper slope, more plastic

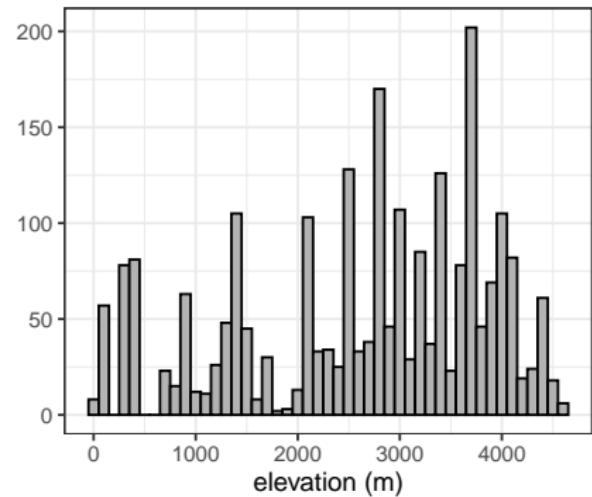
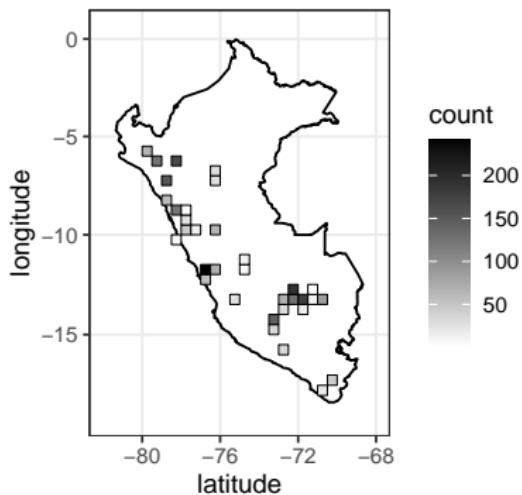


$H_1$ : Respiratory plasticity facilitates niche breadth

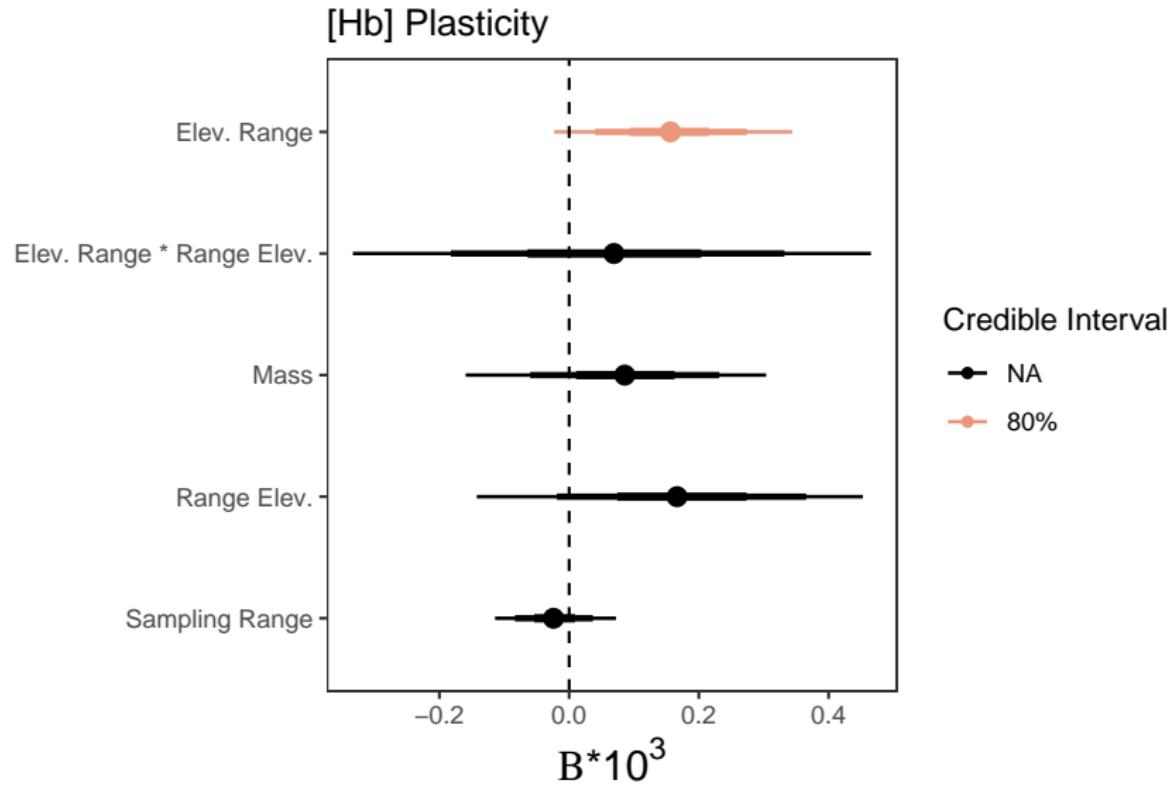


# Methods

- ▶ [Hb] from 2367 individuals of 137 species
- ▶ Bayesian multivariate linear models



# Elevational generalists are more plastic



(Linck et al. *In review*)

We conclude: respiratory plasticity may facilitate elevational range expansion—even if broad elevational ranges aren't stable in the long term  
(Gadek et al. 2017)

## Why it's unsatisfying:

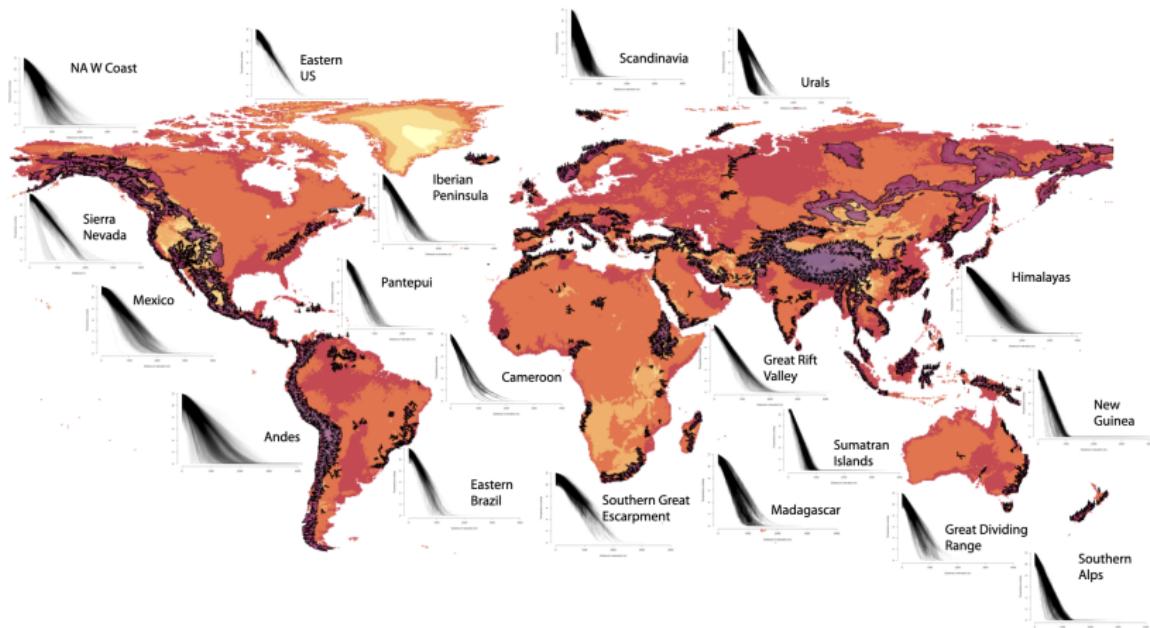
"However if many causes contribute to an observed pattern, none will be eliminated from consideration by a properly designed experiment... The objective of investigation in cases of this sort is not to determine the single cause of a pattern, as no such cause exists, but rather to assign relative importances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

What does the evolution of elevational specialization tell us about adaptation to climate change?

## Acknowledgements:

- ▶ **Collaborators and Coauthors:** Daniel Cadena, Cameron Ghalambor, Ben Freeman, Ignacio Quintero, Juan Parra
- ▶ **Funding:** NSF DBI #1907353, IOS-1457383, DEB-1754821; Banting Postdoctoral Fellowship #379958; University of British Columbia Biodiversity Research Centre Fellowship

# Reduced seasonality in tropical mountains (mostly)

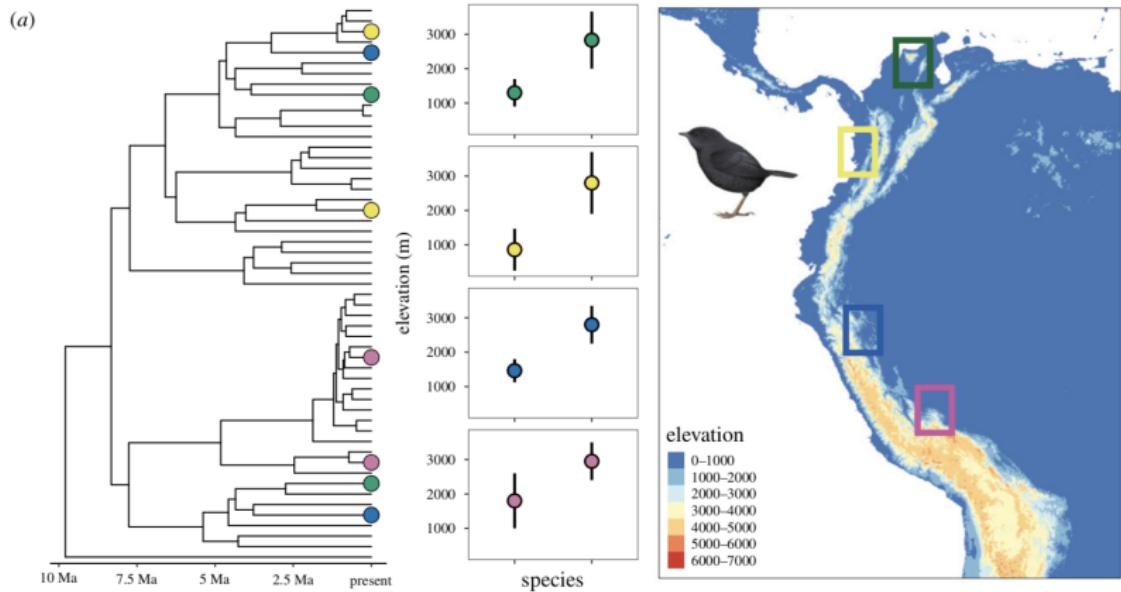


Cadena et al. *In prep*

## Possible lines of evidence

- ▶ **Evolutionary rate of elevational niche shifts**
- ▶ Responses to past climatic changes
- ▶ Rate of upslope movement across latitude

# Niche shifts take time



(Cadena & Céspedes 2020; Linck et al. 2021)

We infer: if elevational range shifts take millions of years in tropical birds, adaptation to new climate niches also a slow process

## Why it's unsatisfying:

"A theory can predict to the extent to which it can describe and explain." It is evident [the source of this quote] is a physicist; no biologist would have made such a statement. The theory of natural selection can describe and explain phenomena with considerable precision, but it cannot make reliable predictions, except through such trivial and meaningless circular statements" (Mayr 1961)

## Biology progresses through incrementally better questions

- ▶ How often do elevational replacements hybridize?
- ▶ What role does genetics play in blood trait plasticity?
- ▶ Are there other genetic constraints on elevational ranges?
- ▶ How do rates of elevational niche evolution compare to geographic range evolution more broadly?
- ▶ What forces lead to niche conservatism?

Thanks!



(Yellow-breasted satinbird, 625-2000m)