

# The origins of diversity in frog assemblages: phylogeny, morphology, performance, and dispersal

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# Why do we see the phenotypic diversity that we see in a given assemblage?

## (1) Environment



versus



Photo: International Polar Foundation

# Why do we see the phenotypic diversity that we see in a given assemblage?

(1) Environment

(2) Important to consider how various aspects of the phenotype are related

– Ecology, morphology, and performance (Arnold 1983; Wainwright 1991)

(3) Historical biogeographic context is necessary to understand how assemblages developed (Losos 1996)

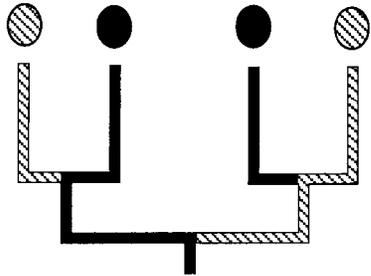
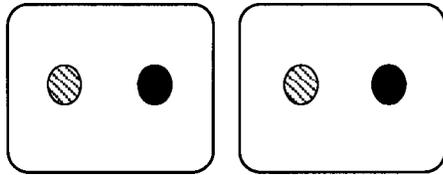
– Diversification within a given location (Schluter and McPhail 1993, Losos et al. 1998, Kornfield and Smith 2000)

– Biogeographic dispersal with little phenotypic change (Ackerly 2003, Stephens and Wiens 2004)

Convergent community structure

region 1

region 2



Convergent adaptive evolution

Diversification  
within a given  
location

# Convergent similarity across assemblages

## MARSUPIALS AND PLACENTALS

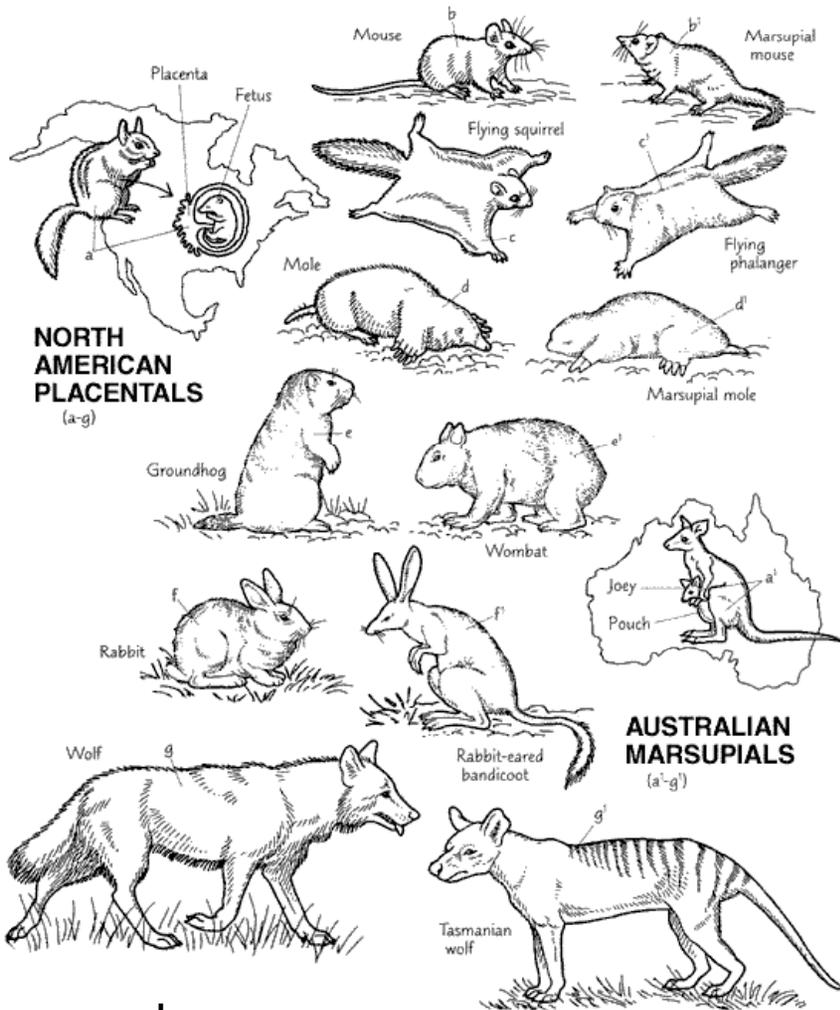
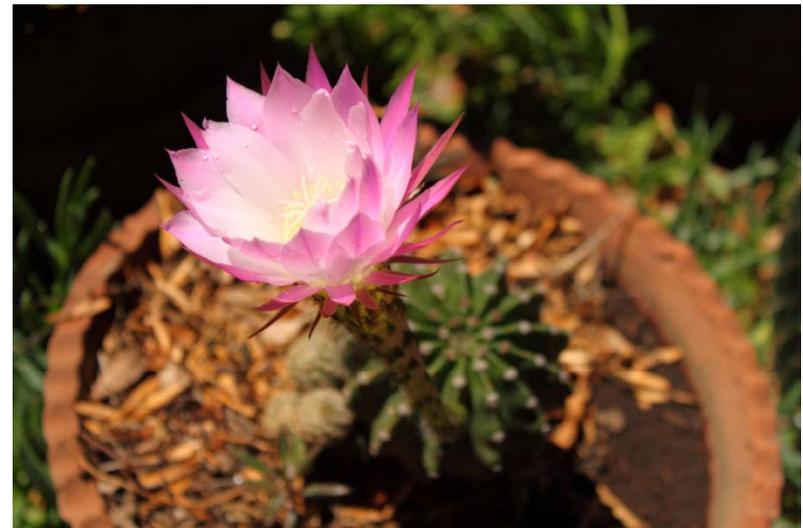
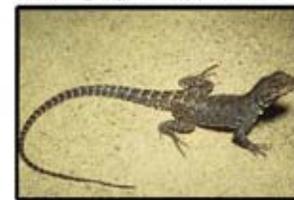
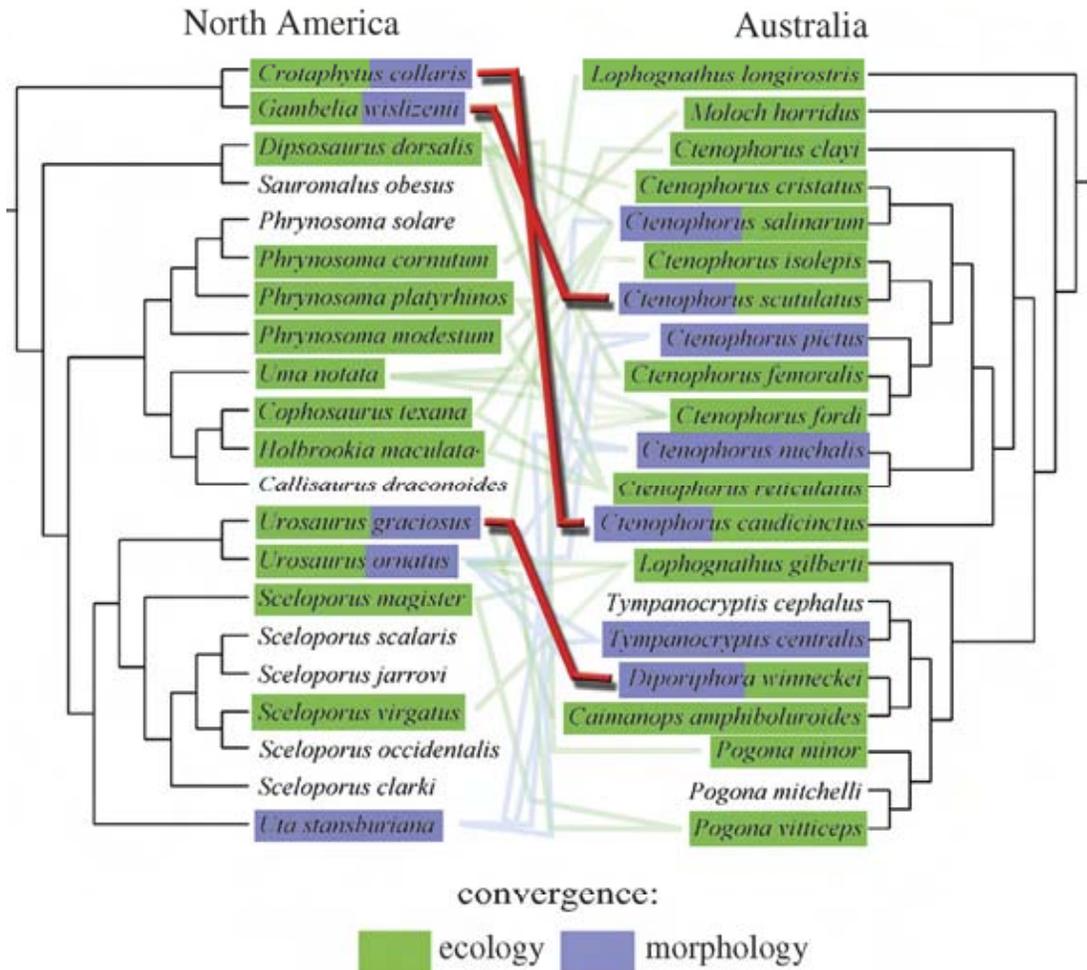


Photo: cactiguide.com



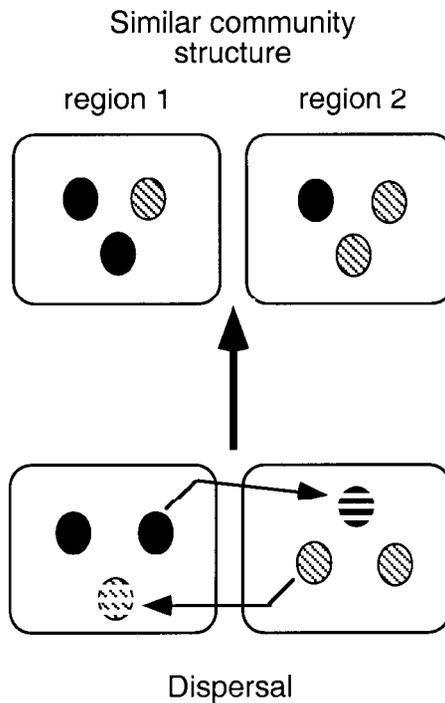
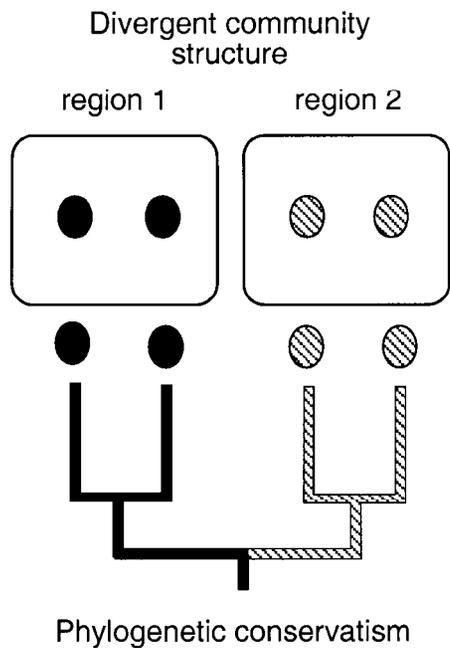
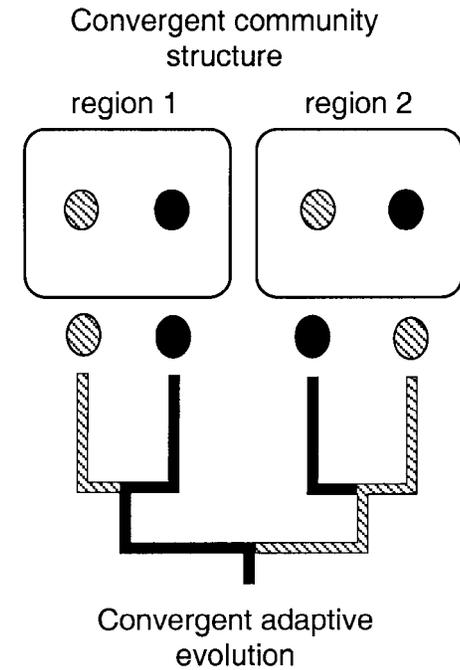
# Convergent similarity across assemblages



At the global scale?

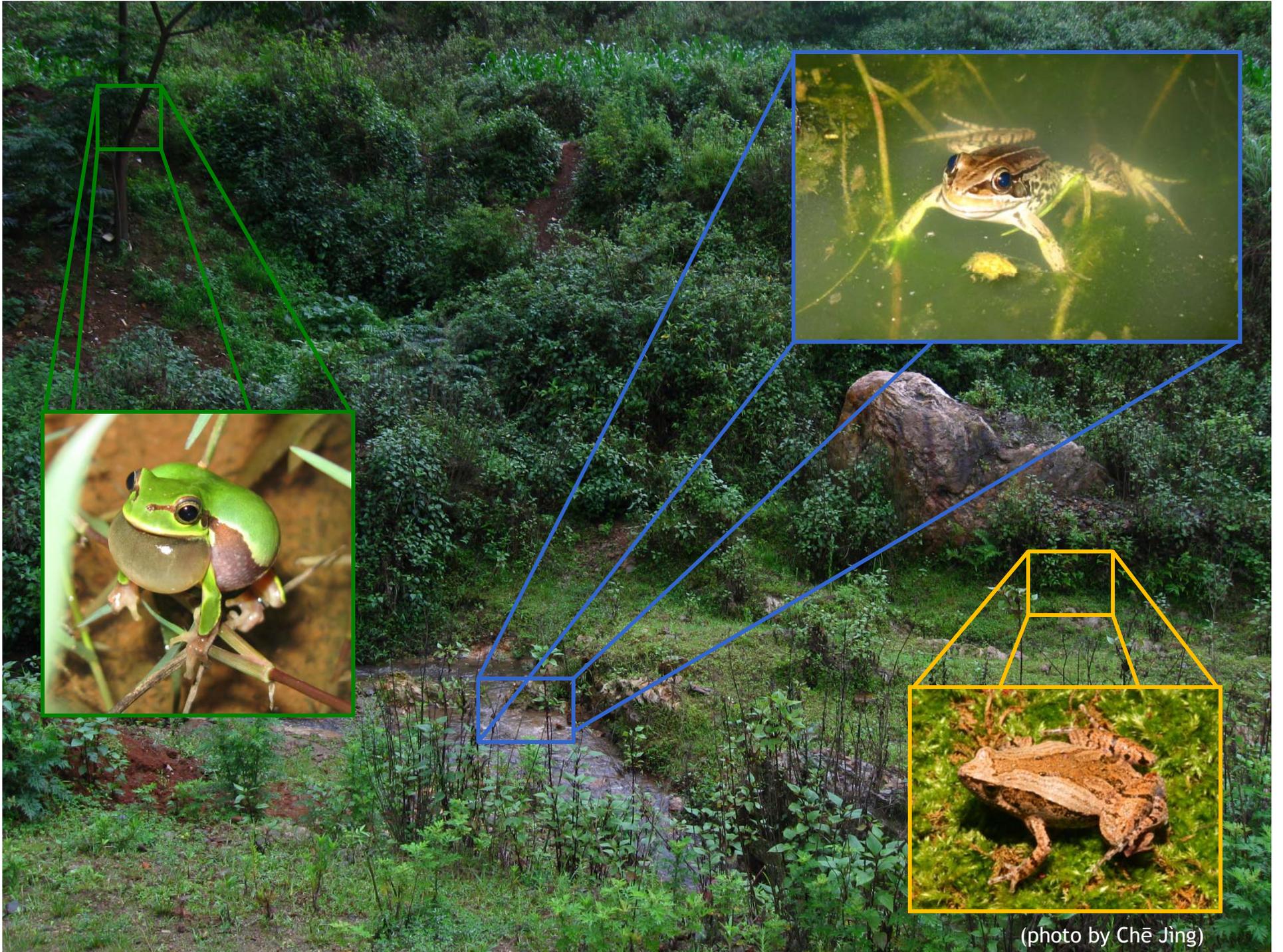


Diversification  
within a given  
location



Biogeographic  
dispersal with little  
phenotypic change





(photo by Chē Jìng)

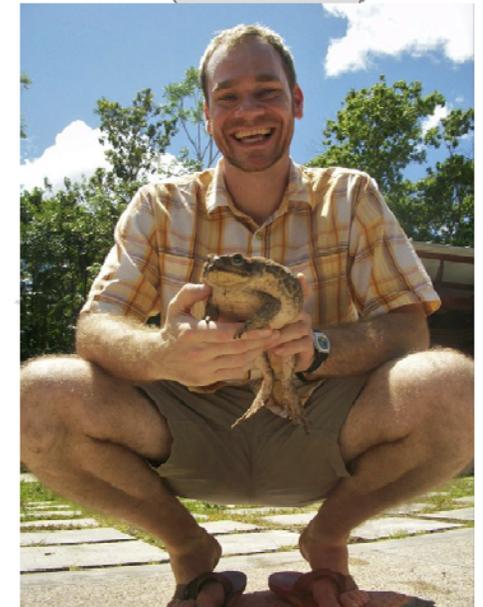
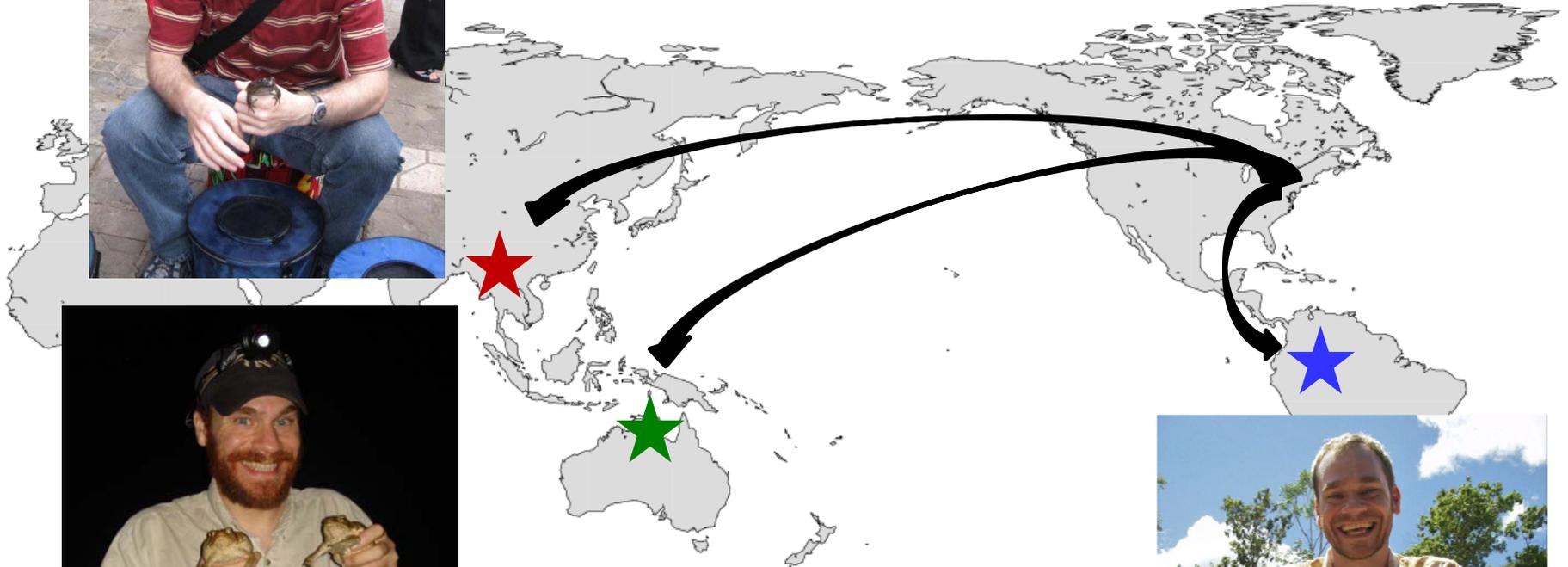


# Herein, I ask:

- (1) Are species that use the same microhabitat around the world also similar in morphology and performance?
- (2) Can species similarity at huge spatial and temporal scales be due to biogeographic dispersal and evolutionary conservatism?
- (3) How do morphology and performance evolve in association with microhabitat transitions in an in situ radiation?



# from 3 assemblages



- (1) Yunnan, China (near Baoshan)
- (2) Amazonas, Colombia (near Leticia)
- (3) Northern Territory, Australia (near Darwin)

# Data: Summary

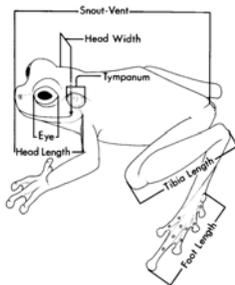
## Performance



## Microhabitat use



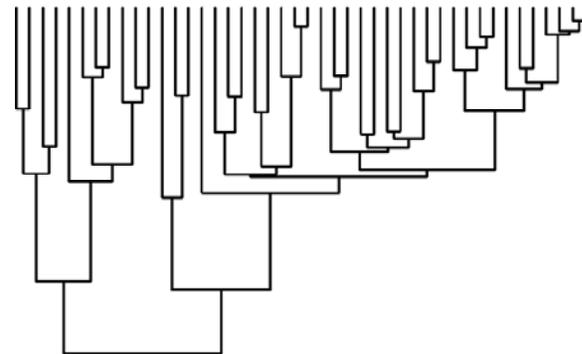
## Morphology



Duellman 2001



## Phylogeny



# Performance data

- Examine the critical feature upon which natural selection acts
- What is important to frogs?
  - Jumping
  - Swimming
  - Clinging ability (to surfaces)
  - Terrestrial endurance
  - Burrowing ability

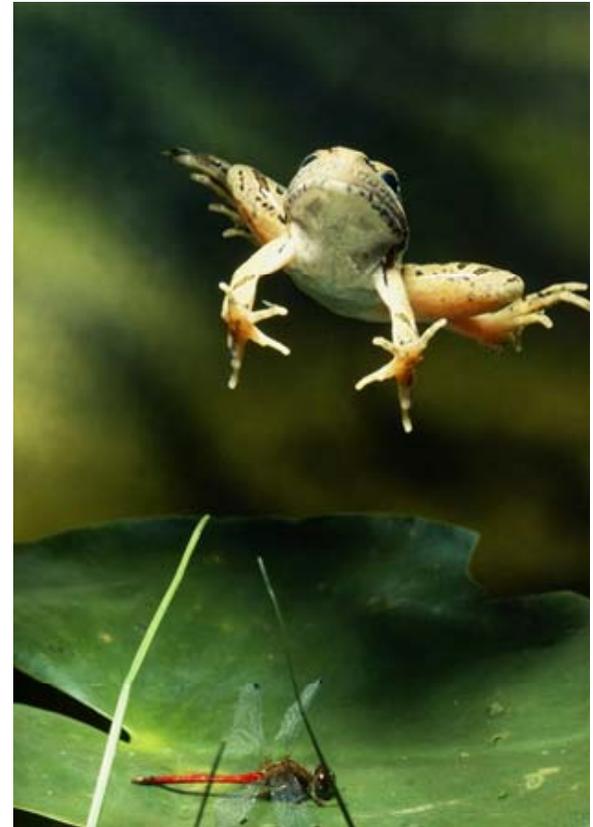


Photo: Bianca Lavies, National Geographic

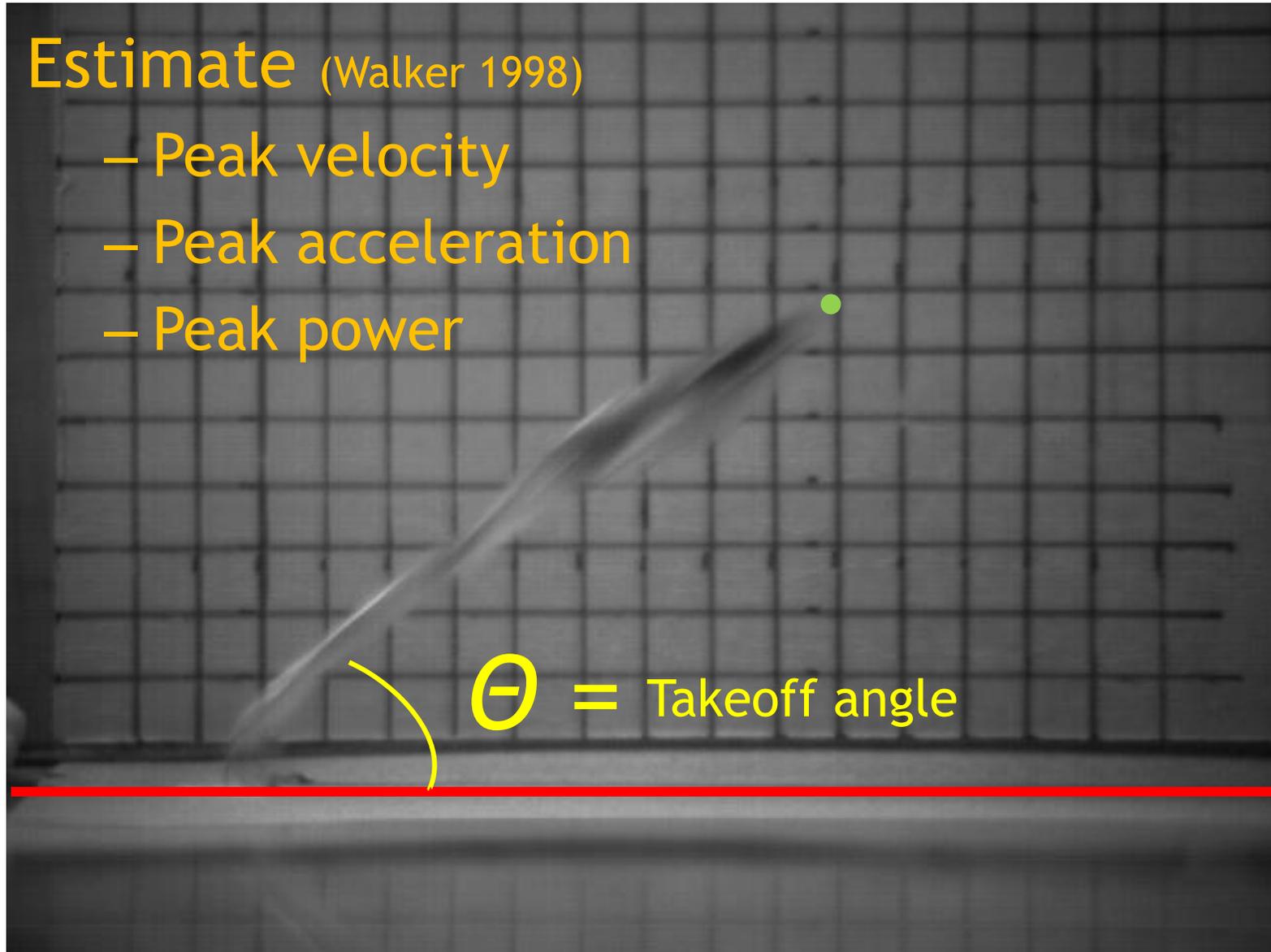
# Jumping



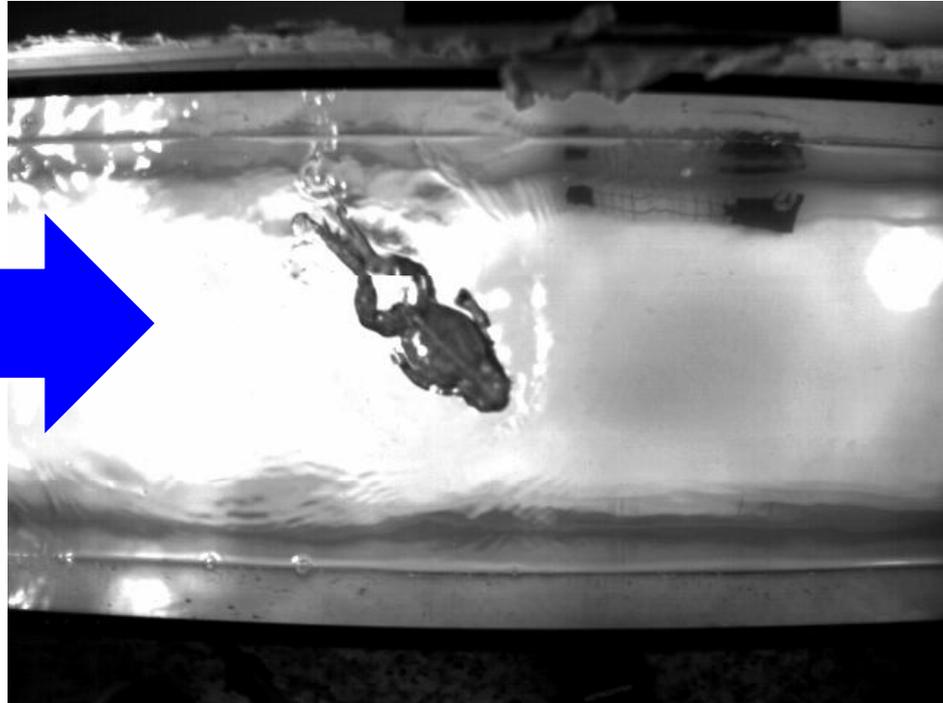
# Measuring performance from videos

**Estimate** (Walker 1998)

- Peak velocity
- Peak acceleration
- Peak power



# Swimming

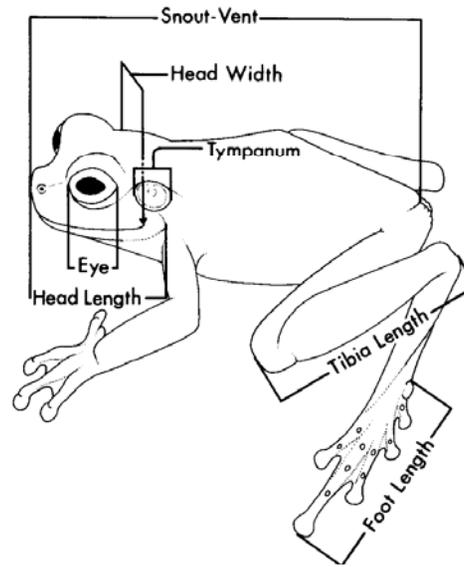


Peak velocity, acceleration, and power are likewise calculated from videos

# Maximum clinging angle



# Morphology



Duellman 2001



Phylogenetic Principal Components (Revell 2009)

PC1: size-related variation

Remaining PCs: size-independent variation

(both performance and morphology)

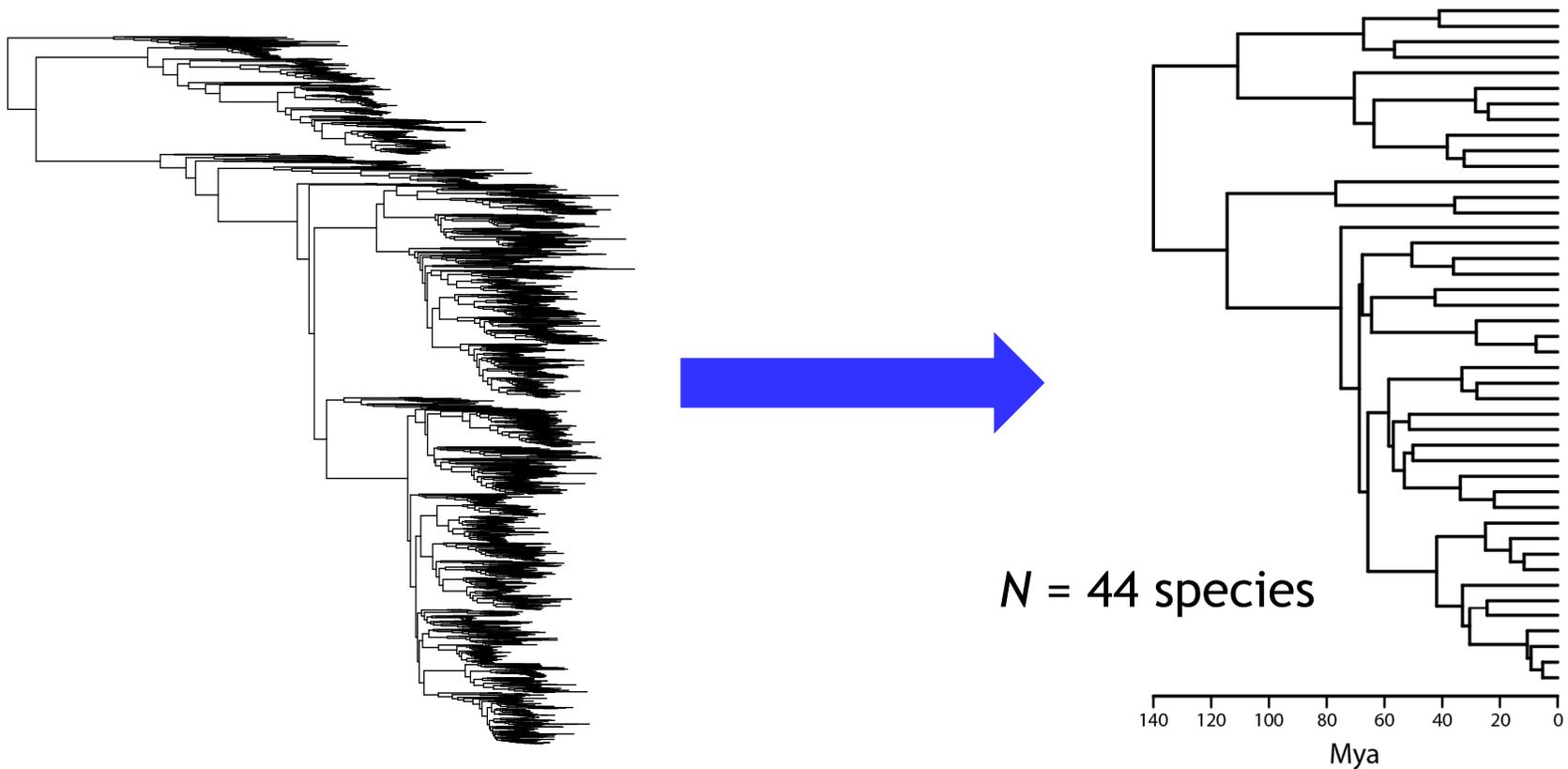
Loadings? Be patient...

# Microhabitat use



# Phylogeny (primary)

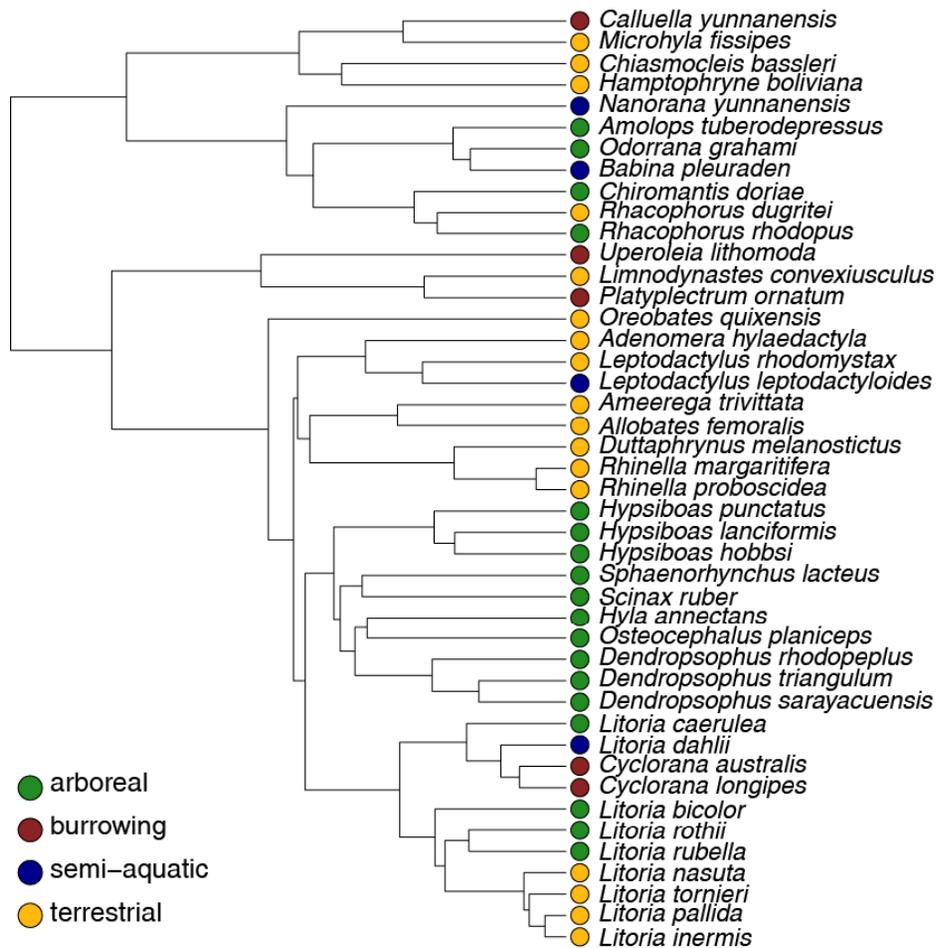
- **Topology: Pyron and Wiens 2011**
- **Branch lengths: BEAST** (Drummond and Rambaut 2007)



# Outline of data analyses

- (1) How is microhabitat use associated with morphology and performance?
- (2) How do morphology and performance evolve when microhabitat is conserved despite great geographic distances?
- (3) How do morphology and performance evolve in association with microhabitat transitions in an in situ radiation?

# Are microhabitat specialists distinctive in morphology and performance?



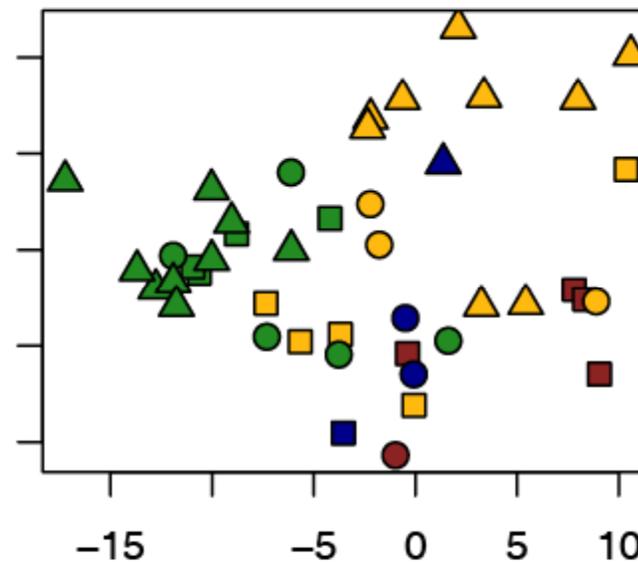
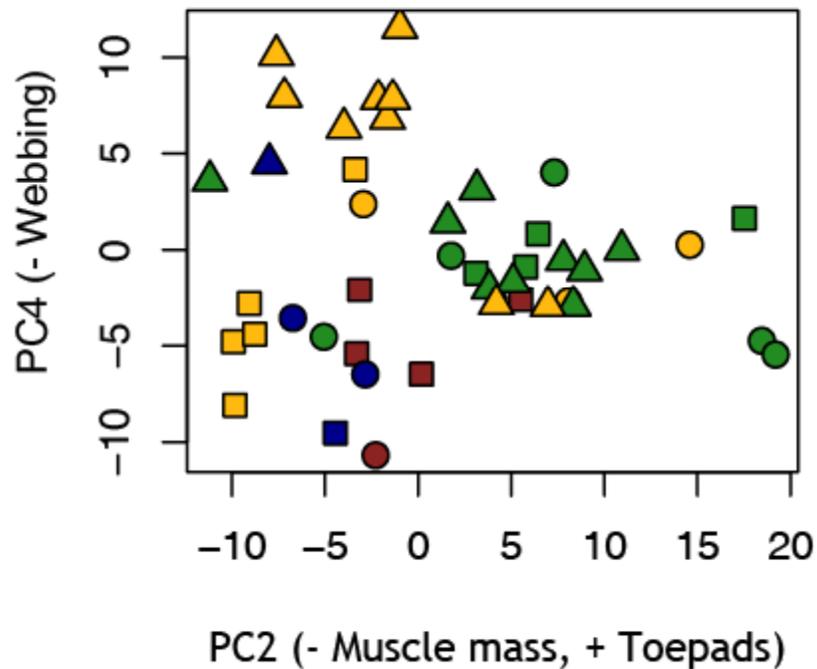
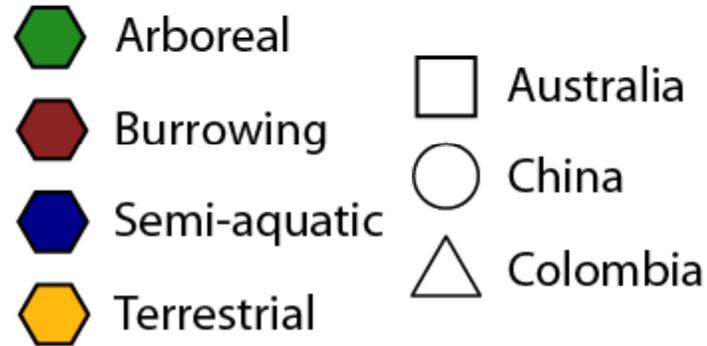
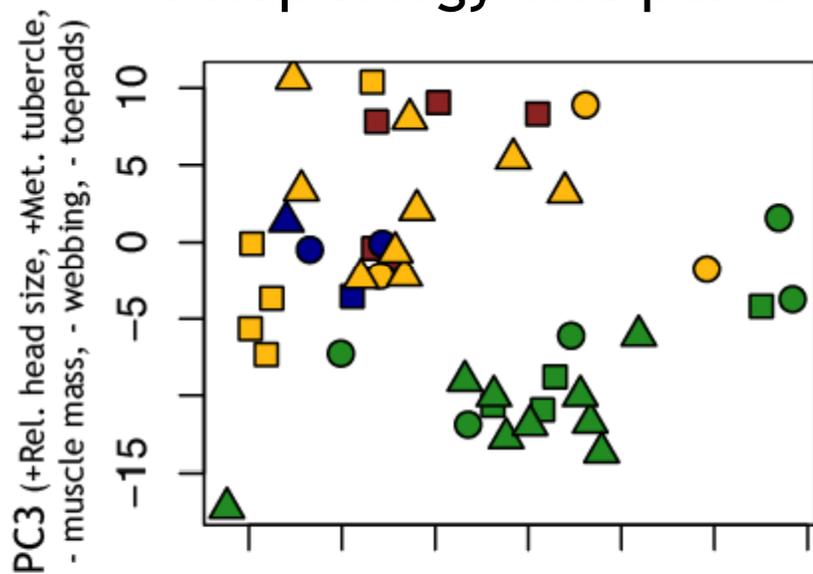
## Multivariate Analysis of Variance (MANOVA)

- Phylogenetically transformed PCA data (Garland and Ives 2000; Blankers et al. 2012)
- Done separately for morphology and performance

# Are microhabitat specialists distinctive in morphology and performance?

## Morphology

(Wilks's  $\Lambda = 0.136$ ,  $P < 0.001$ )

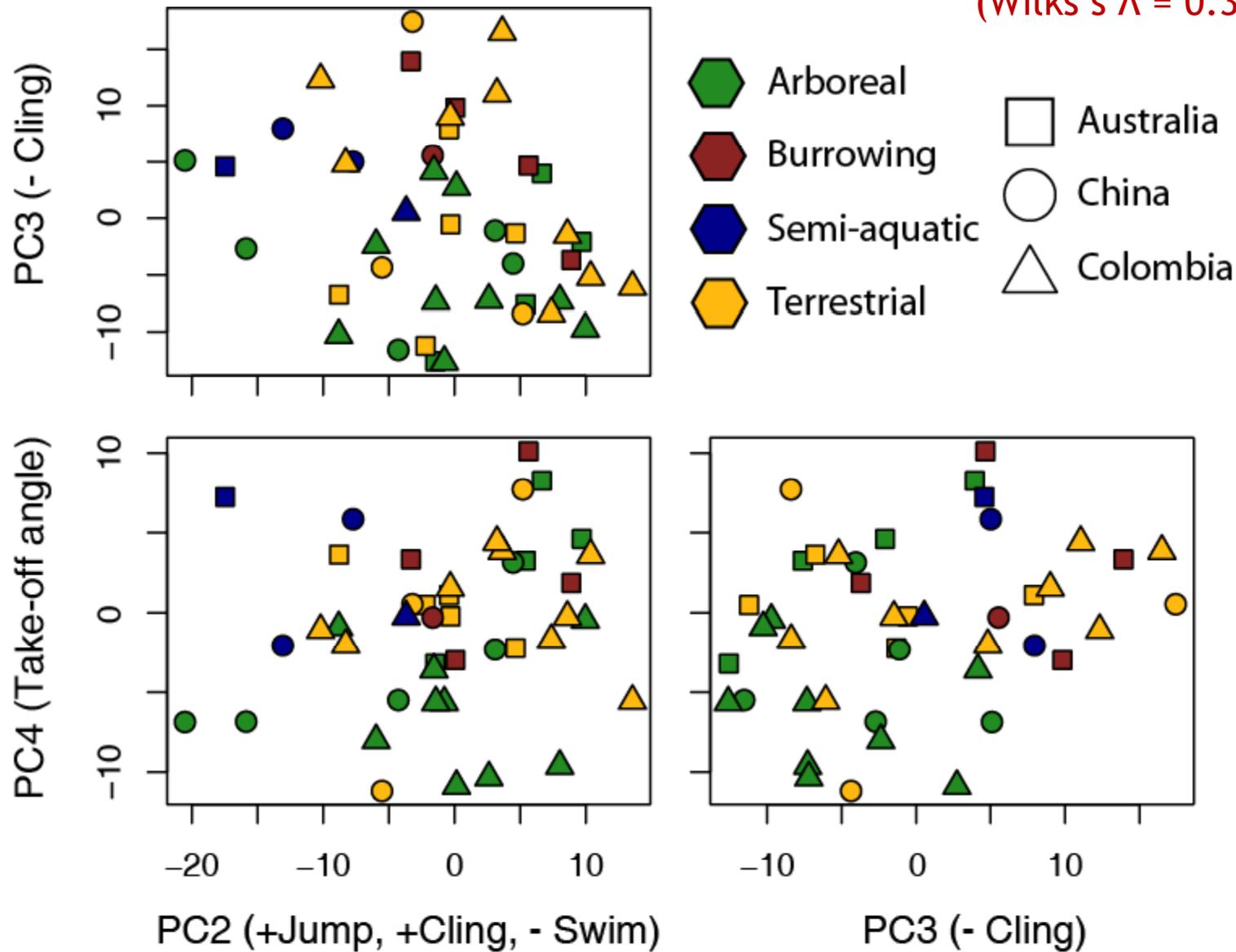


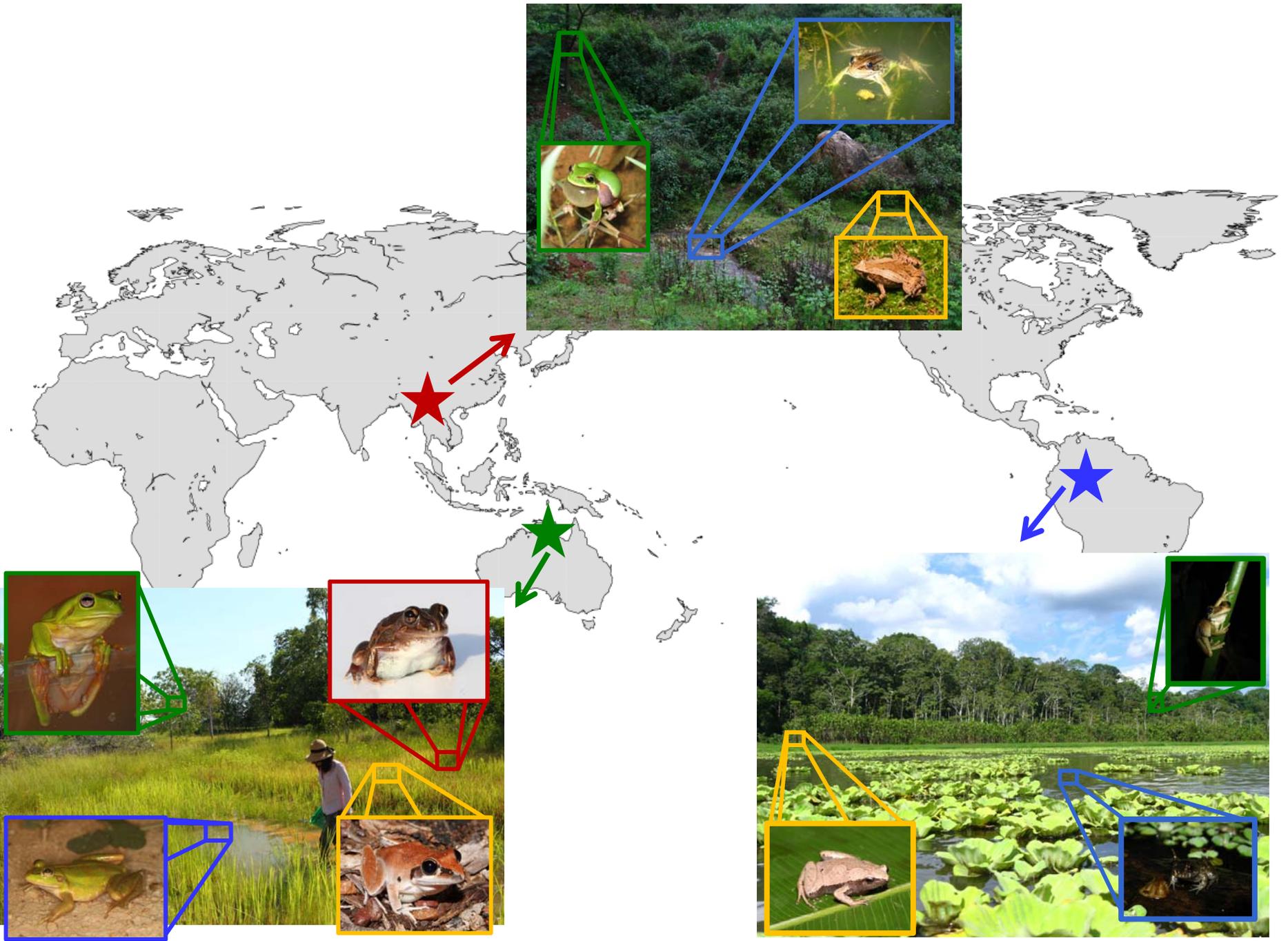
PC3 (+Rel. head size, +Met. tubercle, - muscle mass, - webbing, - toepads)

# Are microhabitat specialists distinctive in morphology and performance?

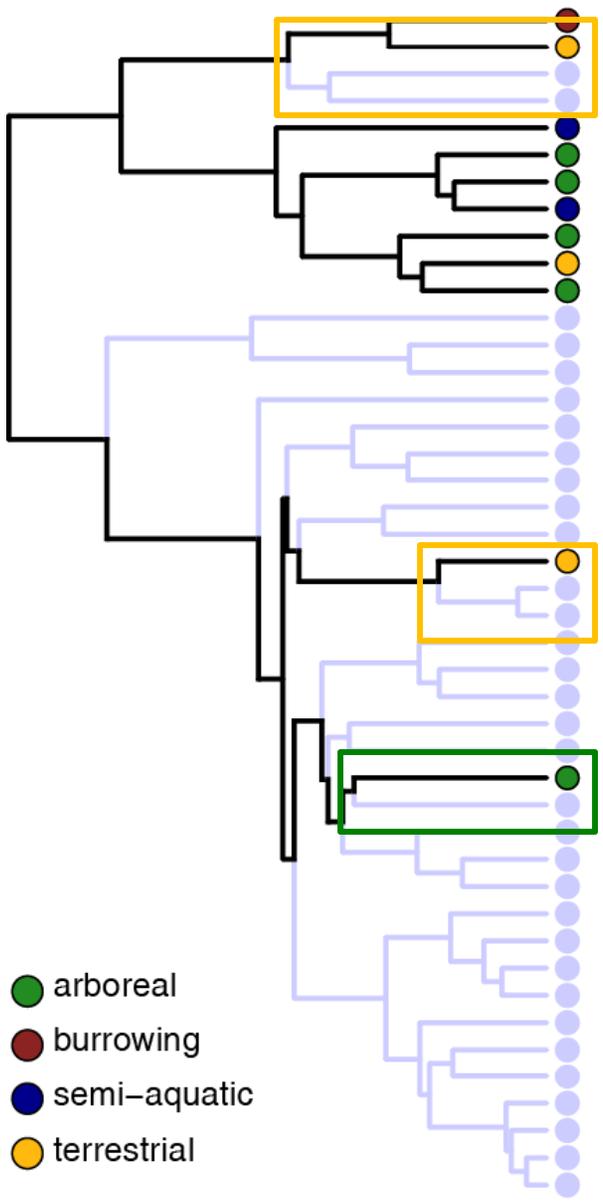
## Performance

(Wilks's  $\Lambda = 0.319$ ,  $P = 0.003$ )





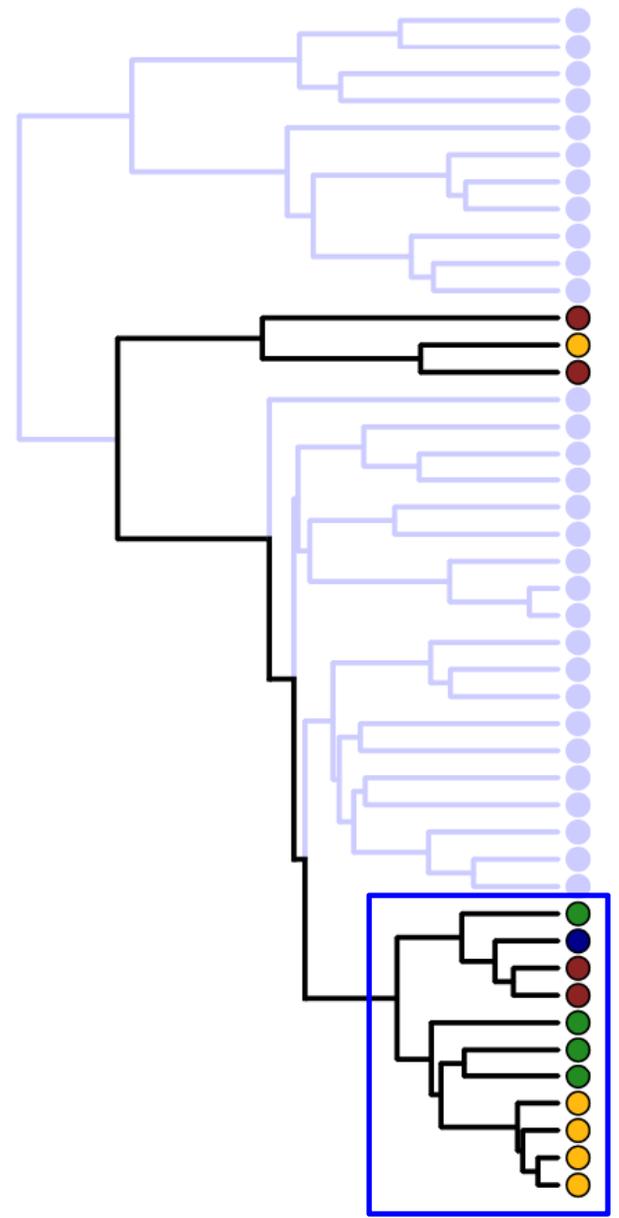
# China



# Colombia



# Australia



- arboreal
- burrowing
- semi-aquatic
- terrestrial

# Outline of data analyses

- (1) How is microhabitat use associated with morphology and performance?
- (2) How do morphology and performance evolve when microhabitat is conserved despite great geographic distances?**
- (3) How do morphology and performance evolve in association with microhabitat transitions in an in situ radiation?

Same microhabitat  
use, geographically  
disparate

Morph.  
distance

Perform.  
distance

Microhylidae

5.3

9.6

Bufo

6.2

9.1

Hyla

21.1

12.0

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Mean terrestrial

15.3

17.8

Mean arboreal

12.1

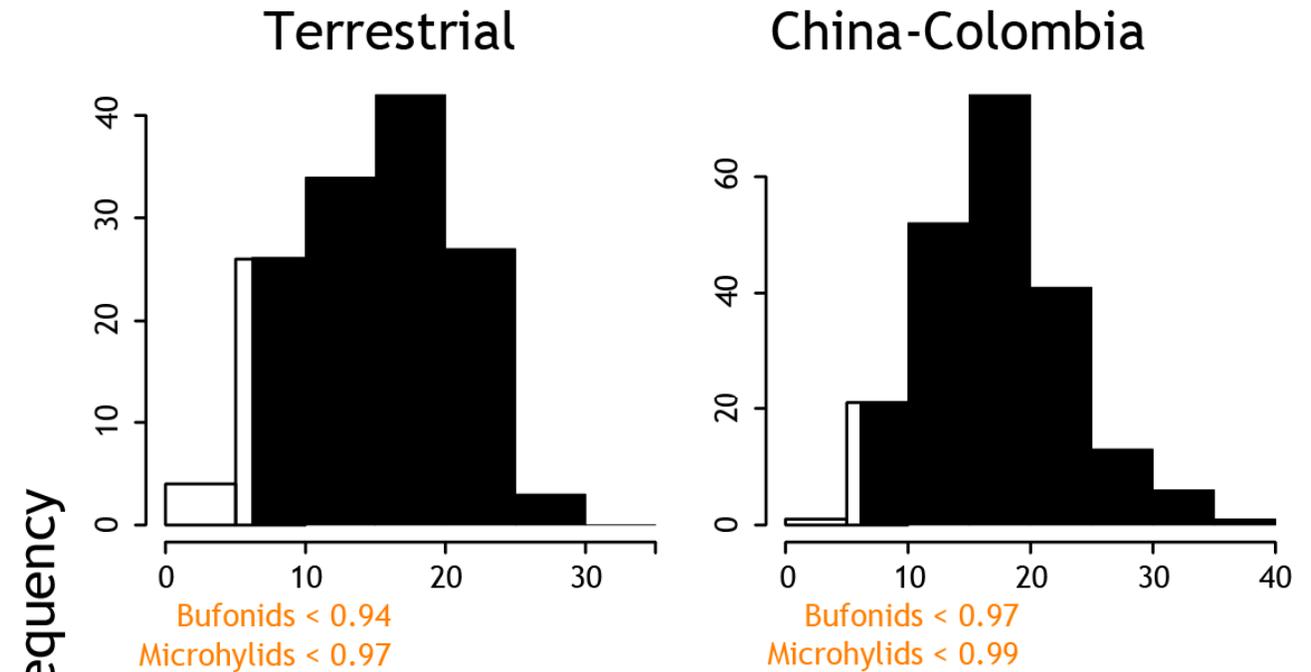
16.5

Mean China-Colombia

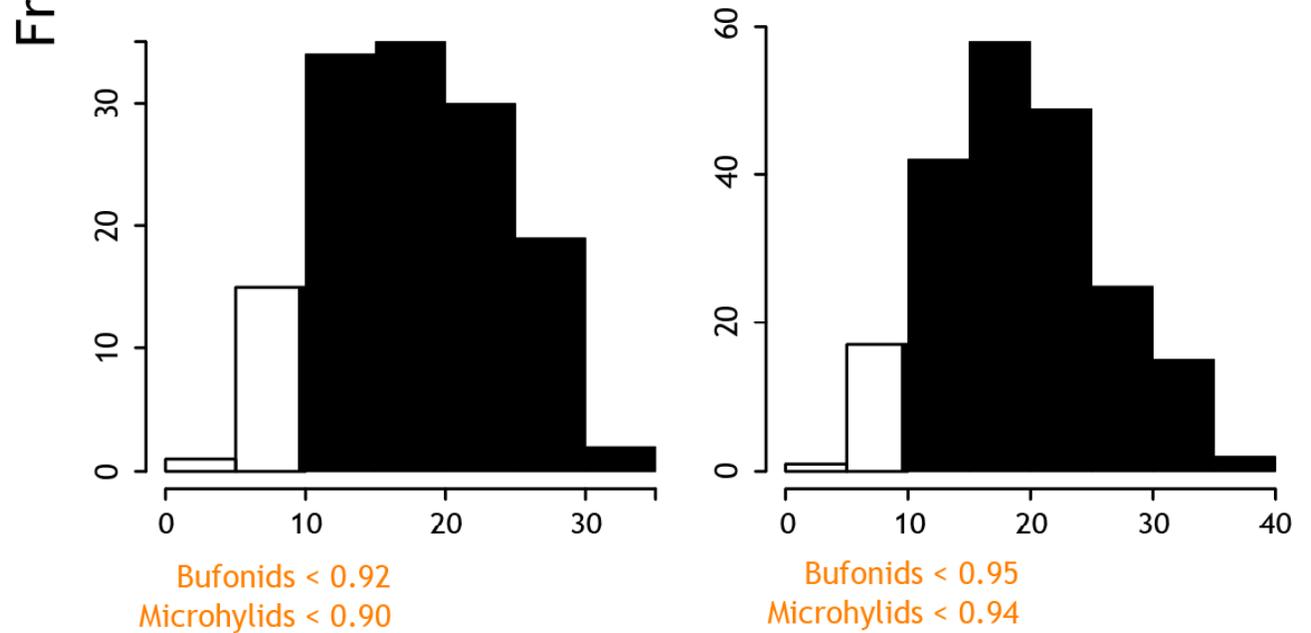
17.2

19.1

Morphological  
pairwise  
distances



Performance  
pairwise  
distances

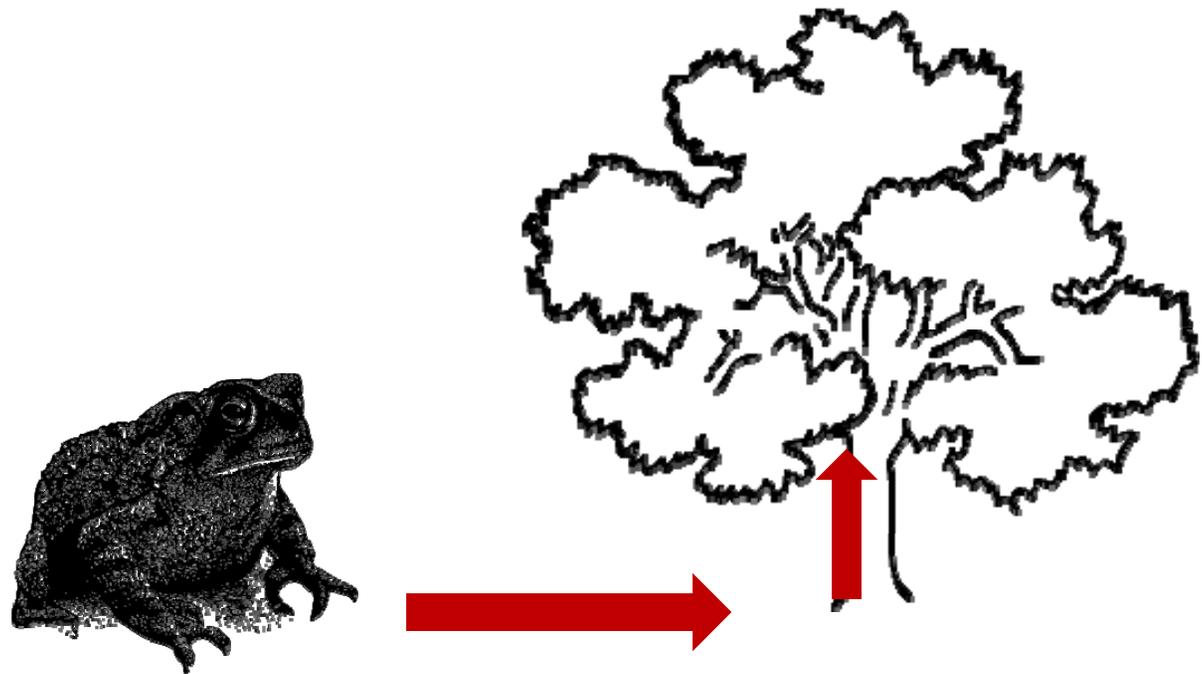


Distance

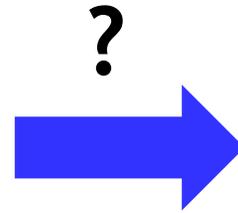
# Outline of data analyses

- (1) How is microhabitat use associated with morphology and performance?
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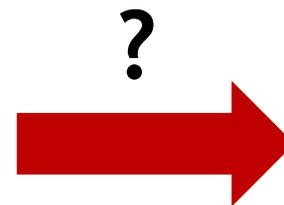
What is the role of prior evolutionary history? Does convergence **completely erase** any traces of history?



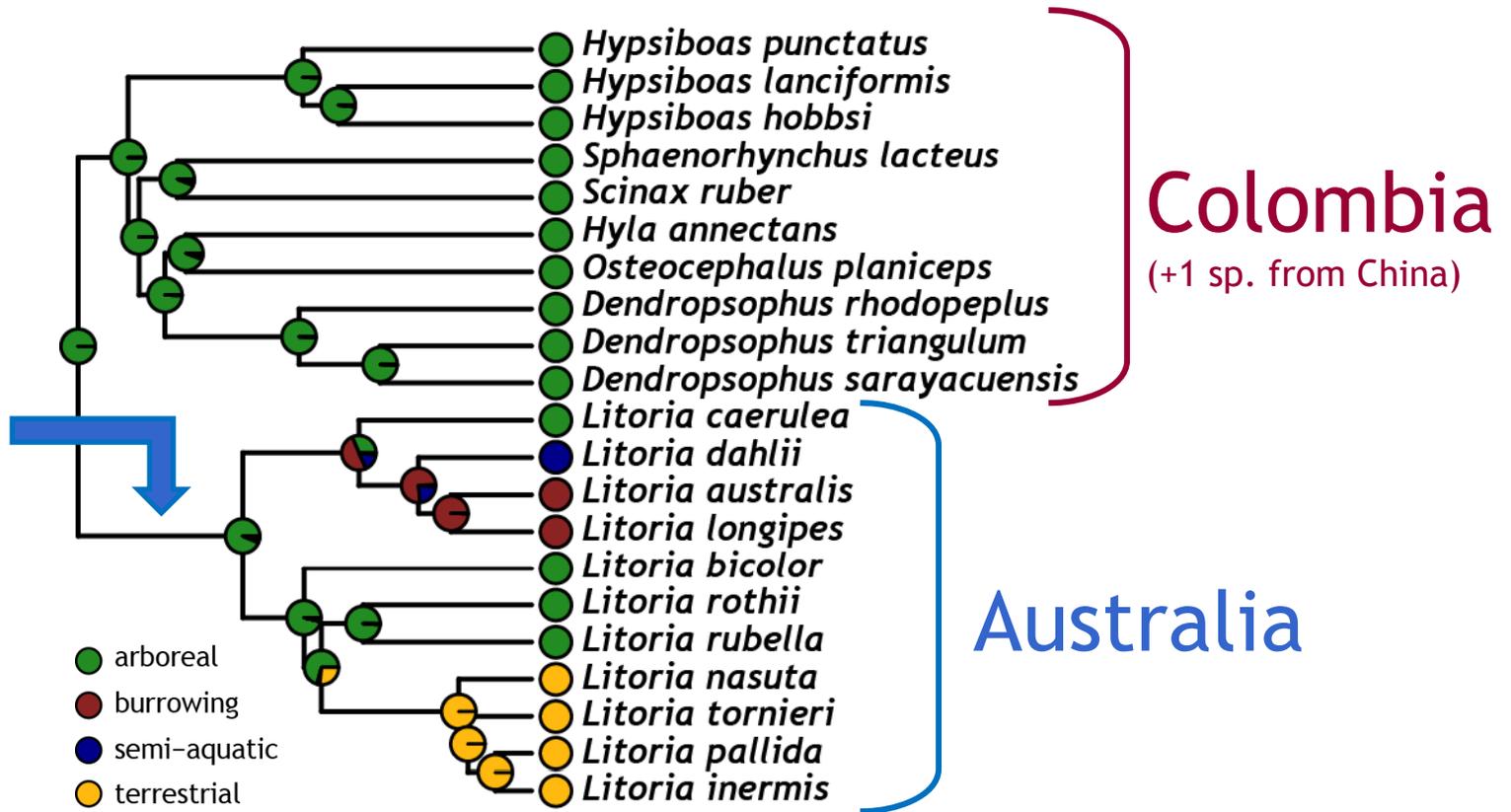
What is the role of prior evolutionary history? Does convergence **completely erase** any traces of history?



Or does prior adaptation to an ancestral environment or resource may generally **leave a footprint** on subsequent evolutionary adaptation?

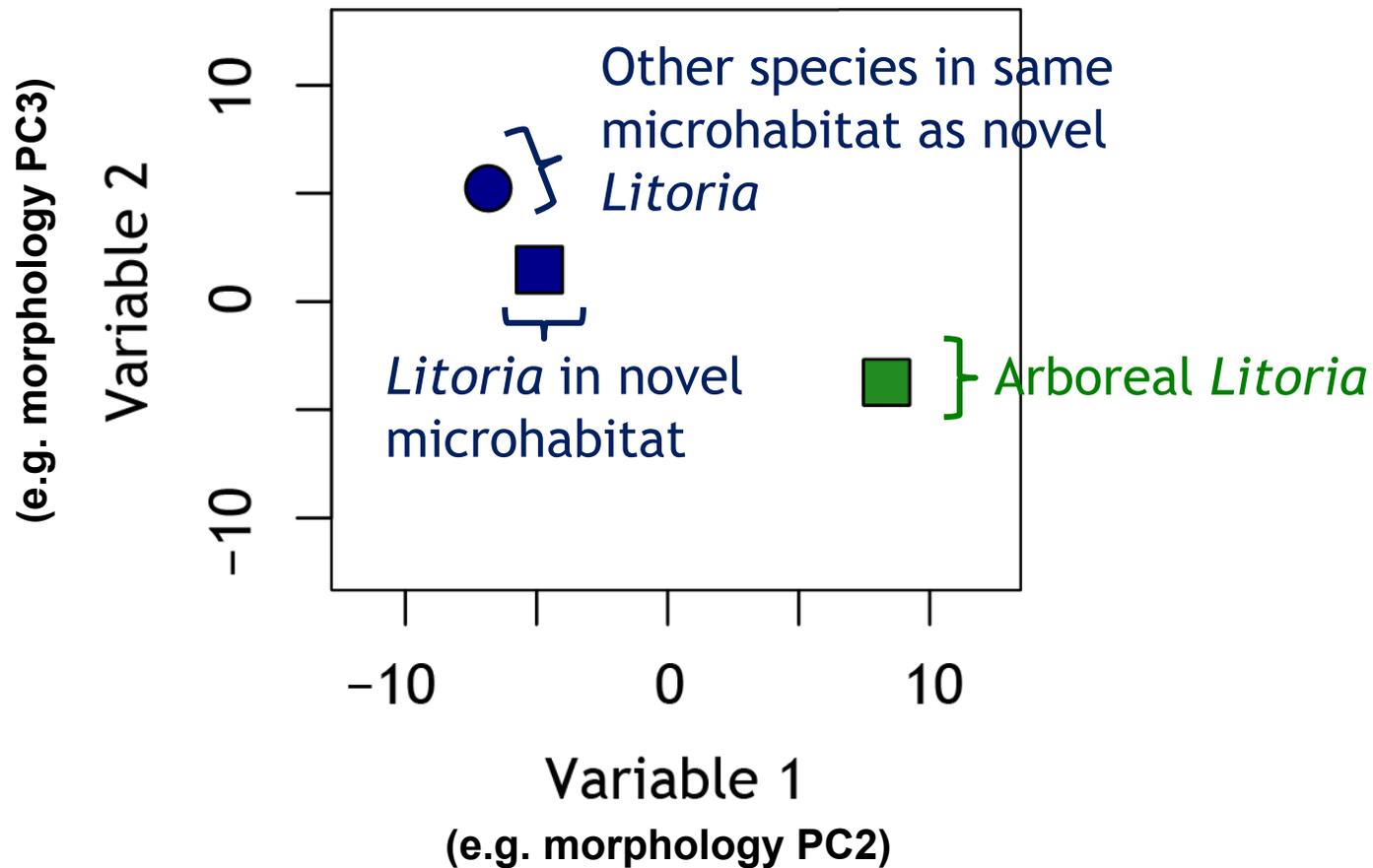


Colonization  
of Australia  
(Wiens et al. 2006)

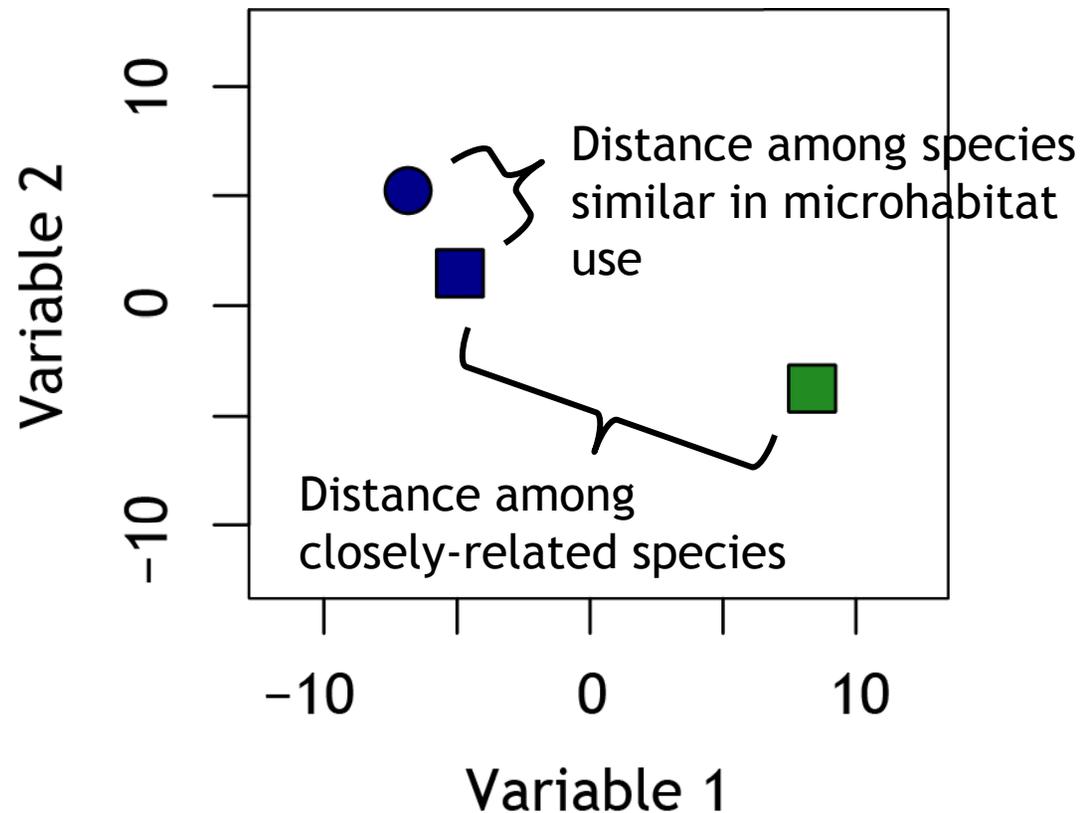


Given this diversification from an arboreal ancestor, how do these “new” microhabitat specialists in the genus *Litoria* compare to other species that are similar in ecology?

Are *Litoria* who are not arboreal more similar to their ancestral type or to other species who share a common ecology?

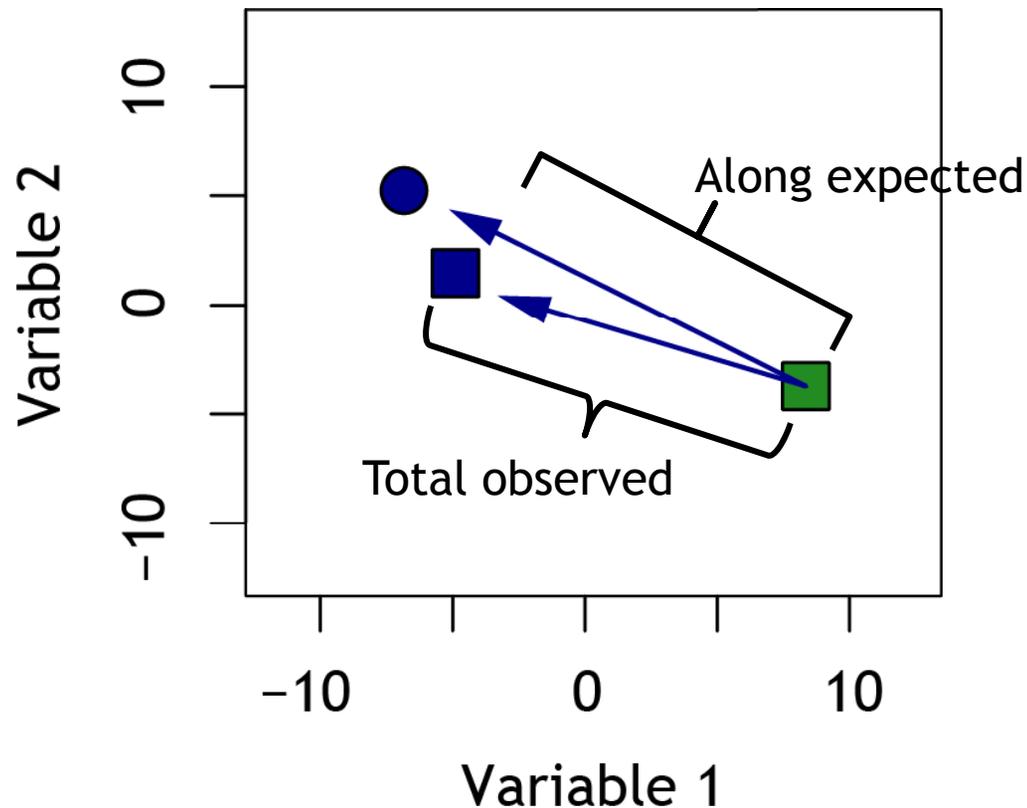


Are *Litoria* who are not arboreal more similar to their ancestral type or to other species who share a common ecology?



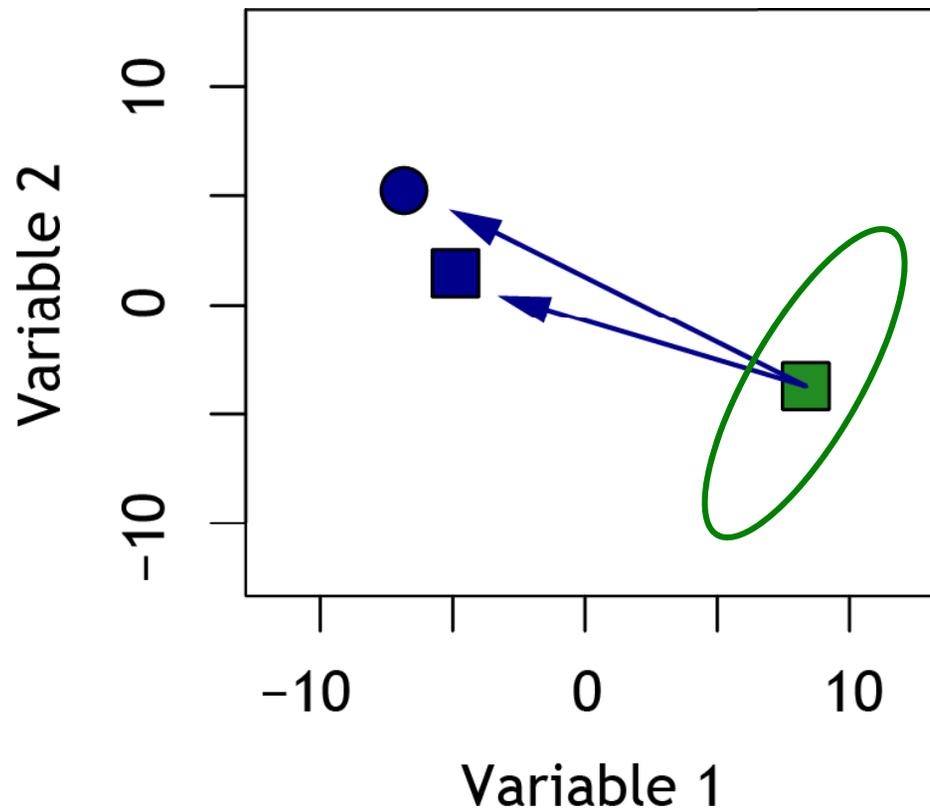
2 ways to compare  
(1) Distance

Are *Litoria* who are not arboreal more similar to their ancestral type or to other species who share a common ecology?



2 ways to compare  
(1) Distance  
(2) Proportion of divergence along expected trajectory relative to total observed divergence ( $p_{obs}$ )

Are *Litoria* who are not arboreal more similar to their ancestral type or to other species who share a common ecology?



2 ways to compare

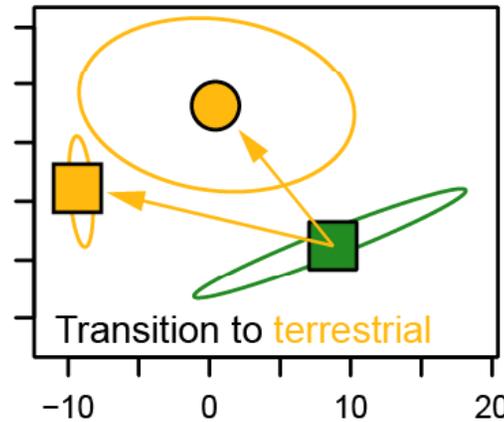
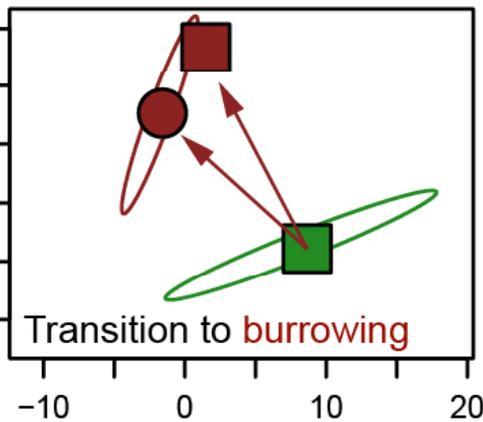
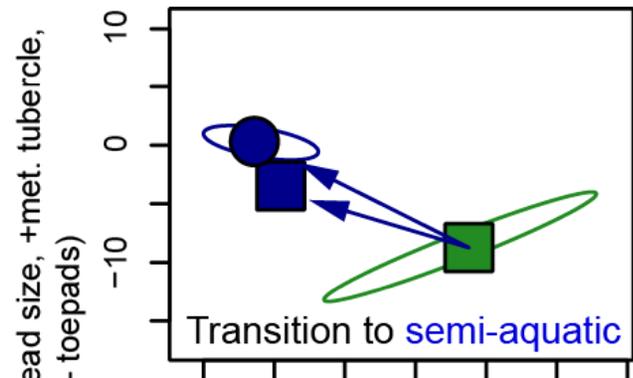
(1) Distance

(2) Proportion of divergence along expected trajectory relative to total observed divergence ( $p_{obs}$ )

# Morphology

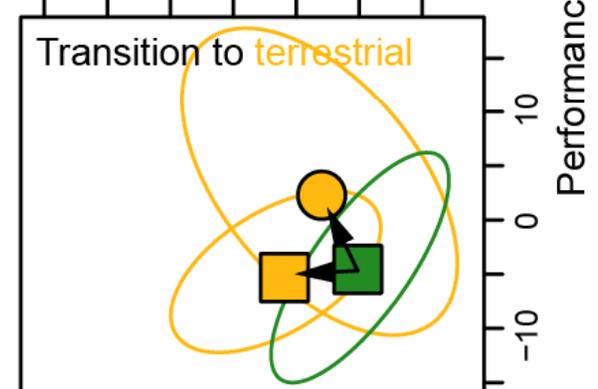
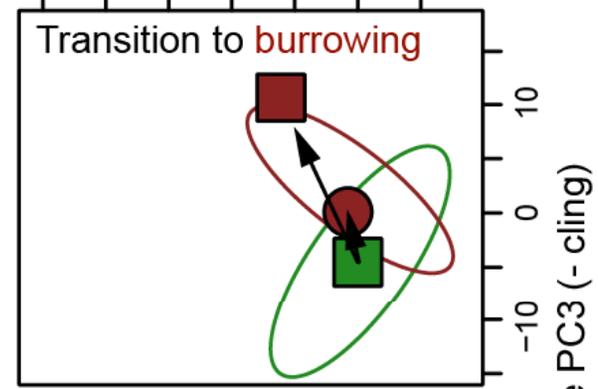
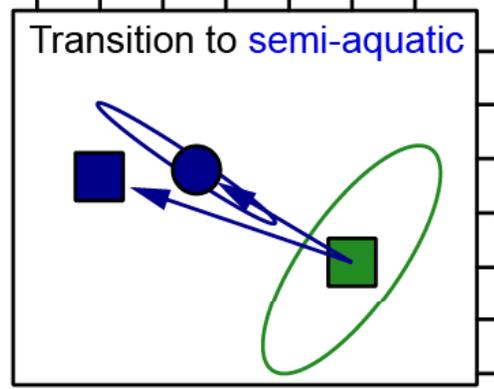
Distance:  $P < 0.001$

$P_{obs}$ :  $P < 0.005$



□ *Litoria*  
○ Non-*Litoria*

Performance PC2 (+jump, +cling, - swim)



# Performance

Distance:  $P < 0.001$

$P_{obs}$ :  $P < 0.003$

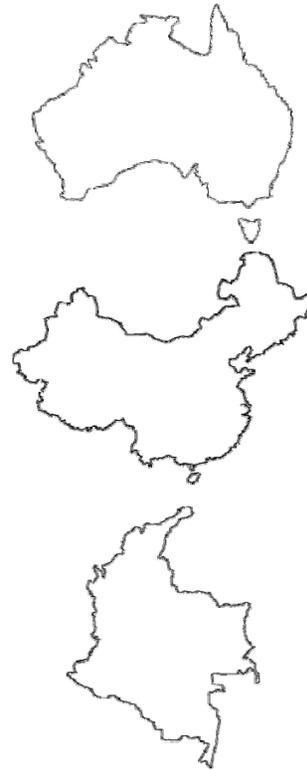
# So what about phenotypic diversity?

Morphological  
variance

133.5

137.8

132.1



Performance  
variance

133.5

172.9

144.8

$P=0.015$



Understanding *why* we see the phenotypic diversity that we see in various assemblages - even at large geographic and temporal scales - depends on considering multiple pathways

➔ Understanding *why* we see the phenotypic diversity that we see in various assemblages depends on considering both:

(1) No geographic change with much diversification

## China



## Australia



➔ Understanding *why* we see the phenotypic diversity that we see in various assemblages depends on considering both:

- (1) No geographic change with much diversification
- (2) Geographic change with little diversification

China

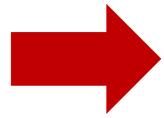
Colombia

Microhylidae  
(67 million years)



Bufoidea  
(28 million years)





Take home message: the **factors** that we should study to understand phenotypic diversity across assemblages will depend on **how** that diversity **developed over time**

- (1) No geographic change with much diversification
  - How does adaptive radiation happen?
  - What are the roles of competition, predation, mutualism, etc.?
  - How common is sympatric speciation?
- (2) Geographic change with little diversification
  - What factors affect long-distance dispersal?
  - Why do we see conservatism in some groups versus much evolution in others?
  - What role does non-adaptive allopatric speciation play?

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