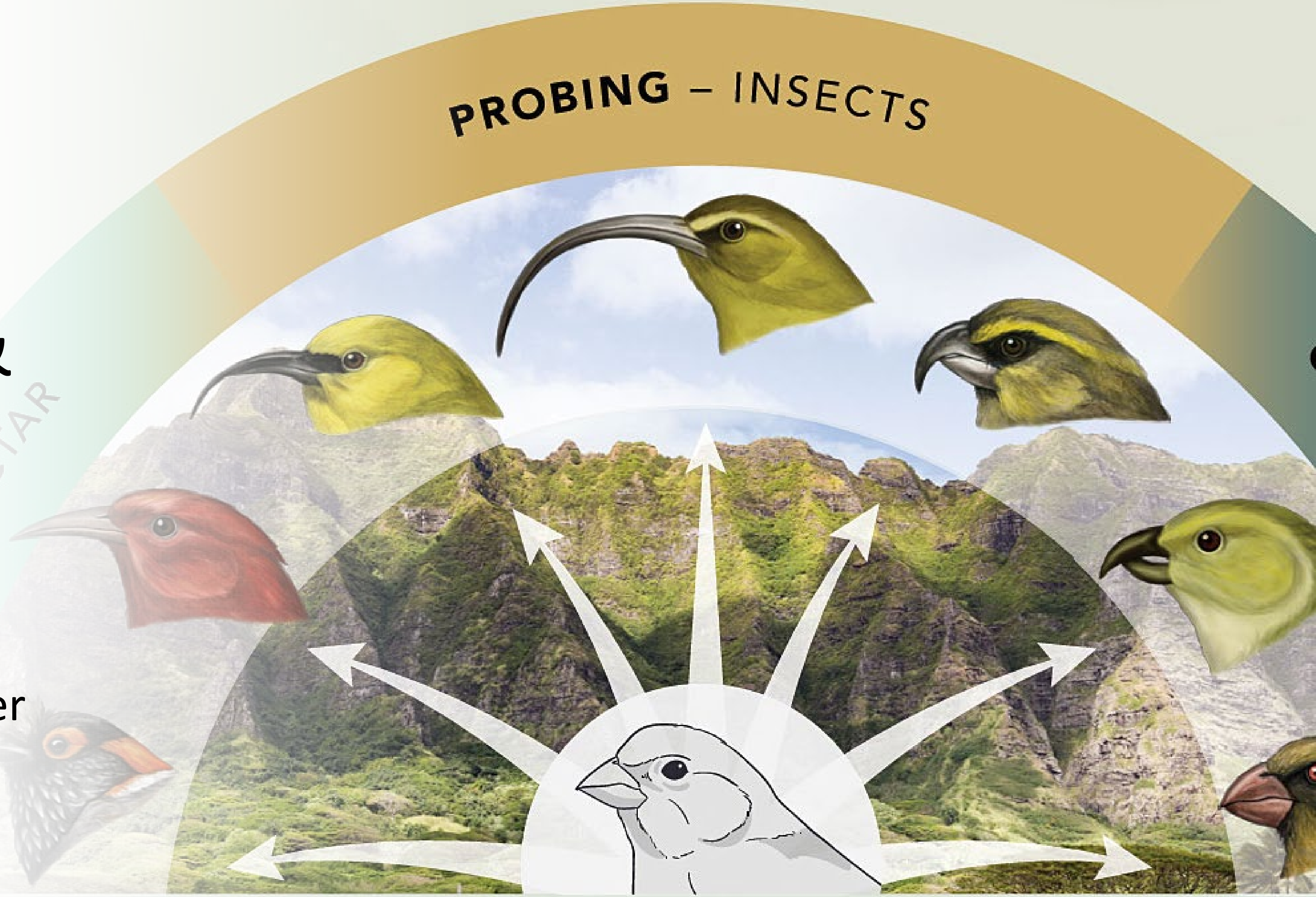
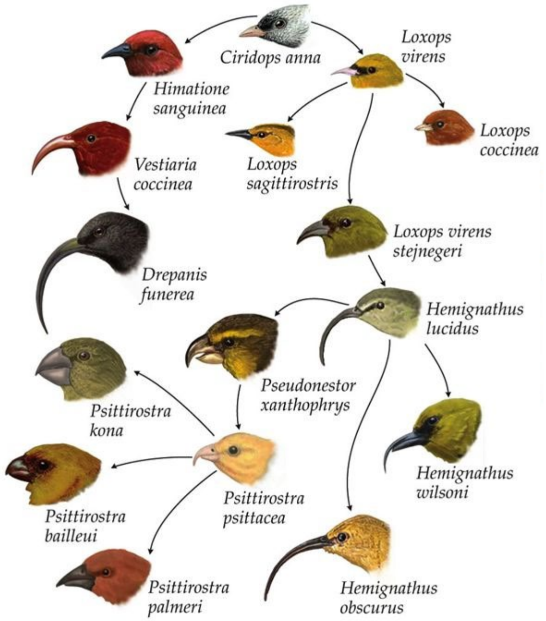
# Adaptive Radiation & Ecological Speciation

Adapted from Neil Rosser

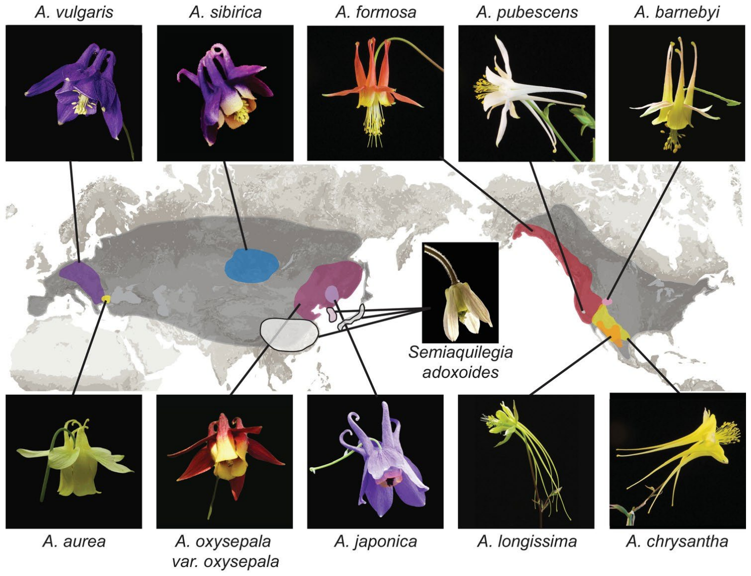
(OEB 140 2022)



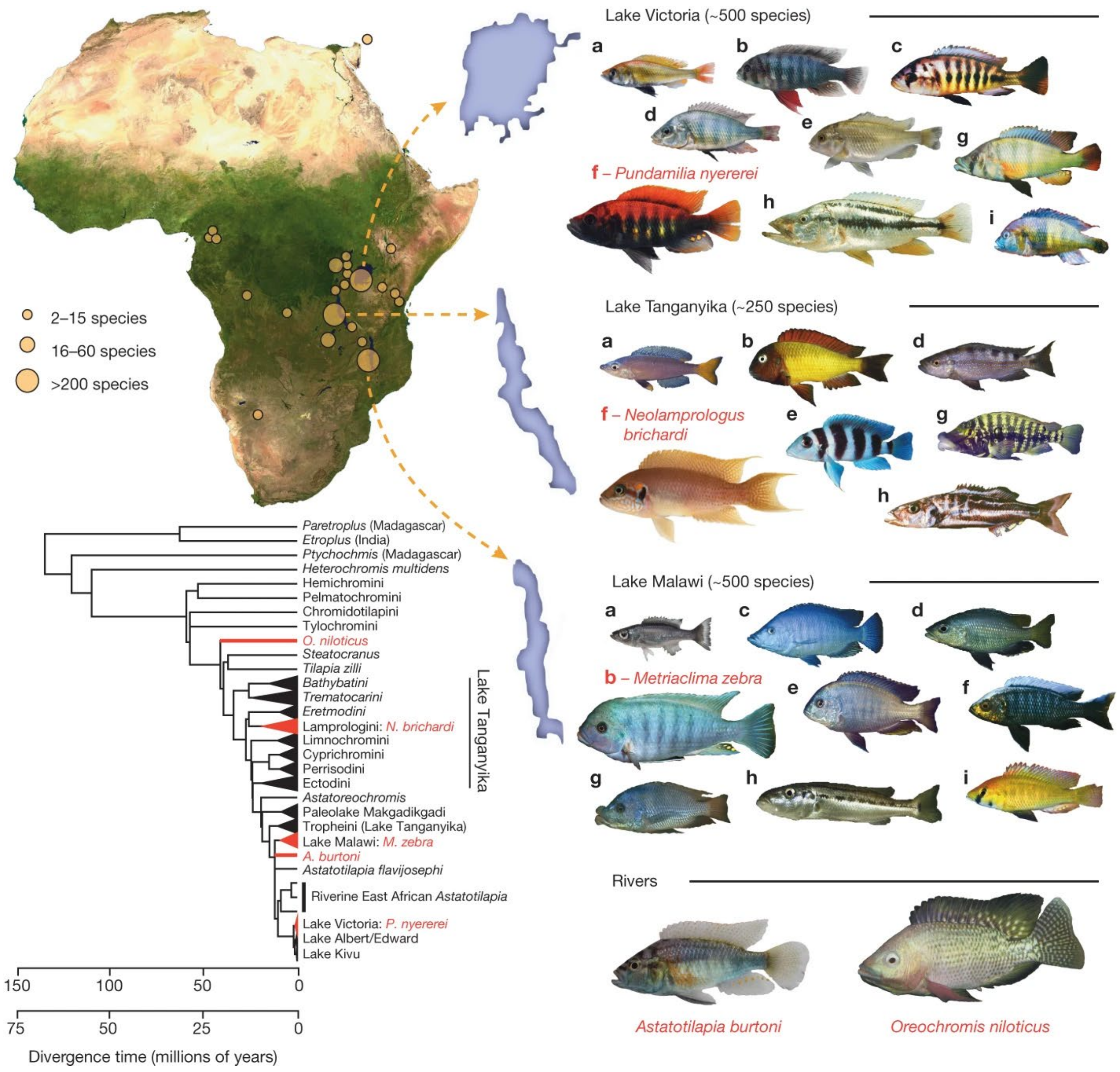
## Hawaiian Honeycreepers




## *Aquilegia* (columbines)



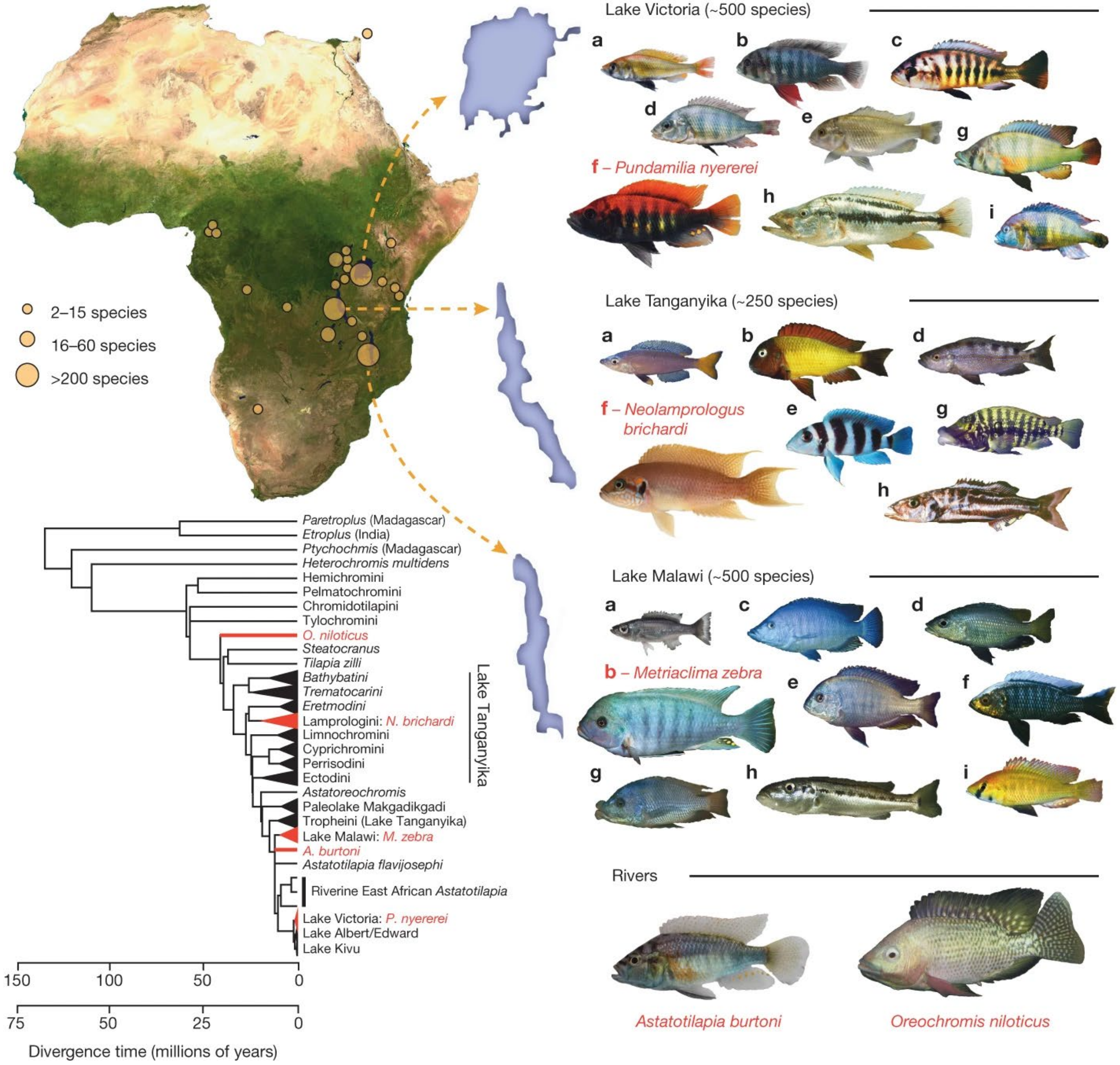

## African cichlid fishes



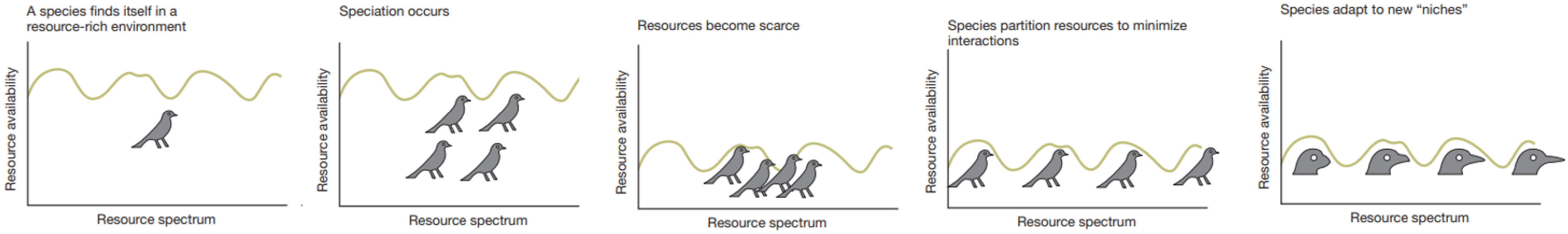
# Why are adaptive radiations interesting?

The high phenotypic diversity coupled with high species richness make them ideal for studying adaptation and speciation

Some people think most biodiversity is the product of such adaptive radiations.

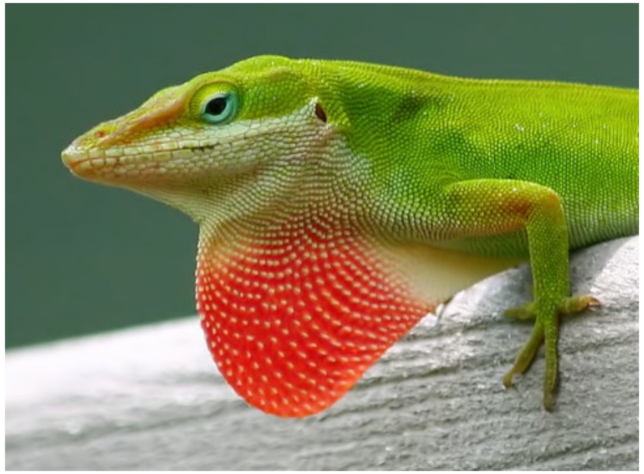


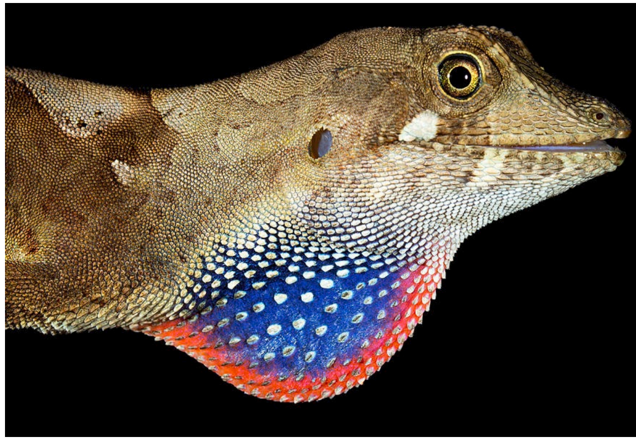
# What is the process by which adaptive radiation occurs?

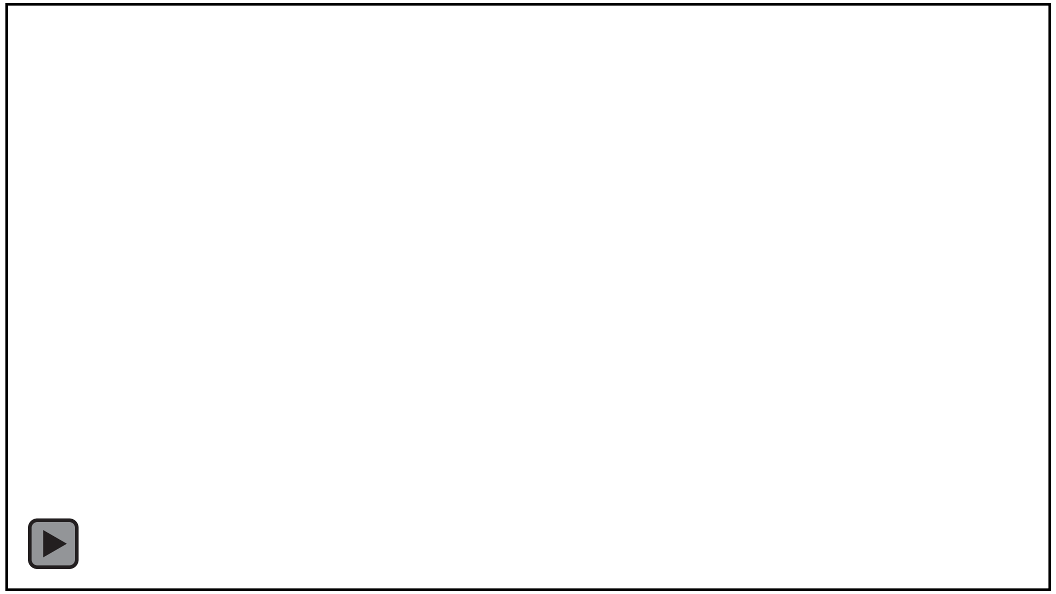


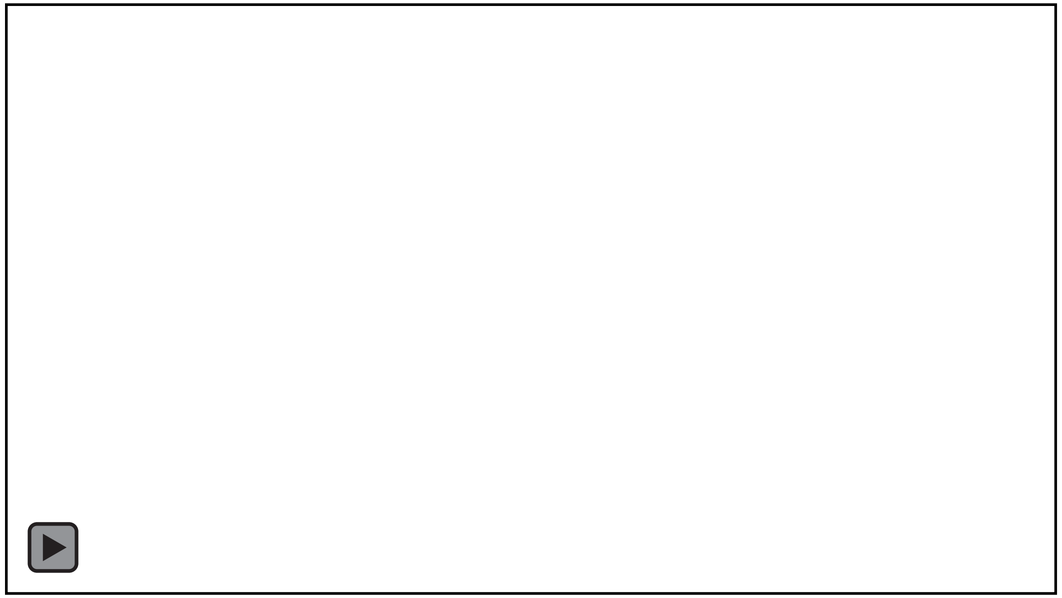

The result is a set of species specialized to use different parts of the resource base (the **resource competition hypothesis).**

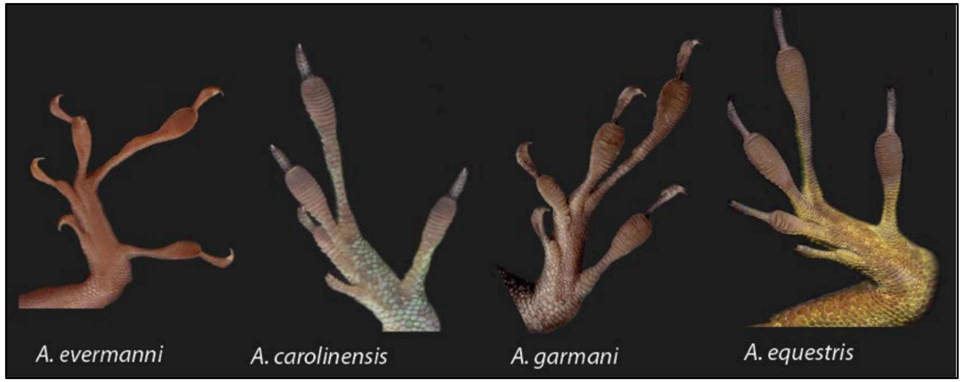
# A classic case study - Anoles from Caribbean

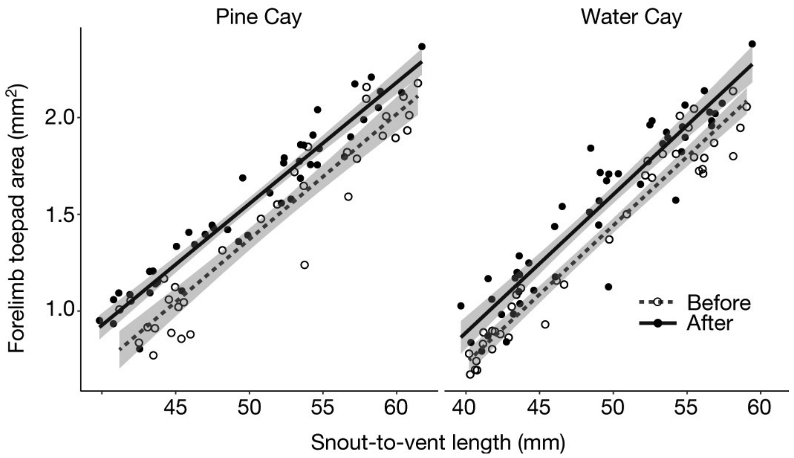






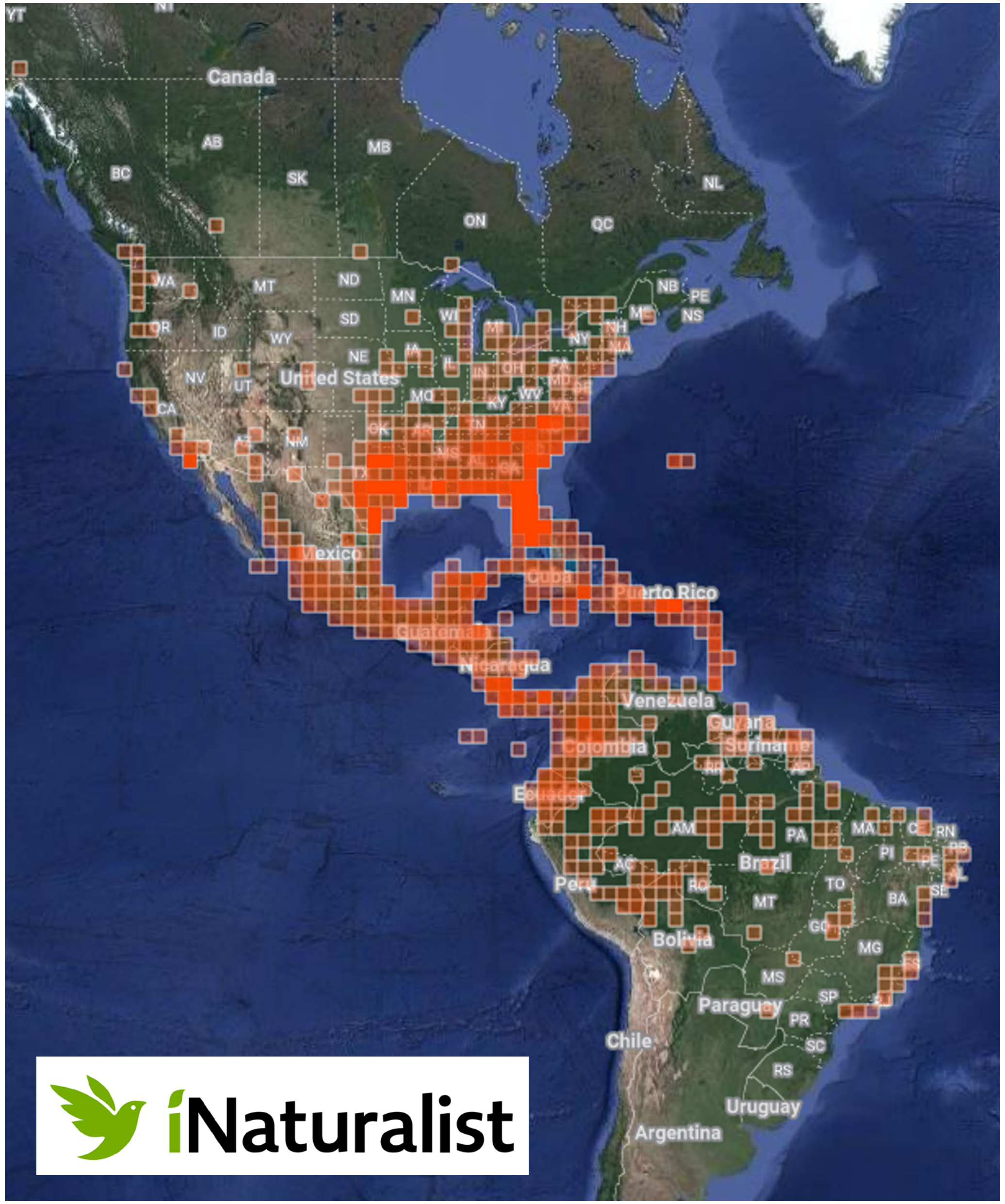


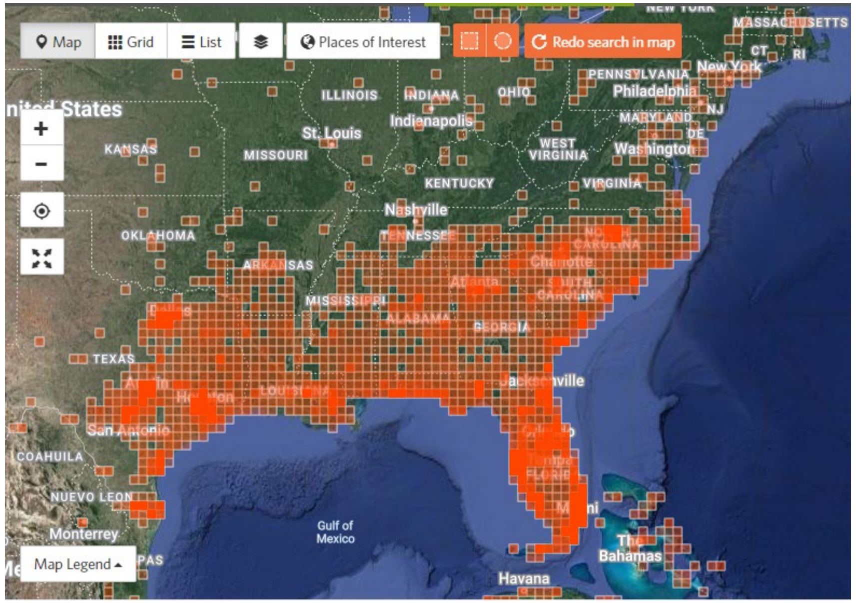


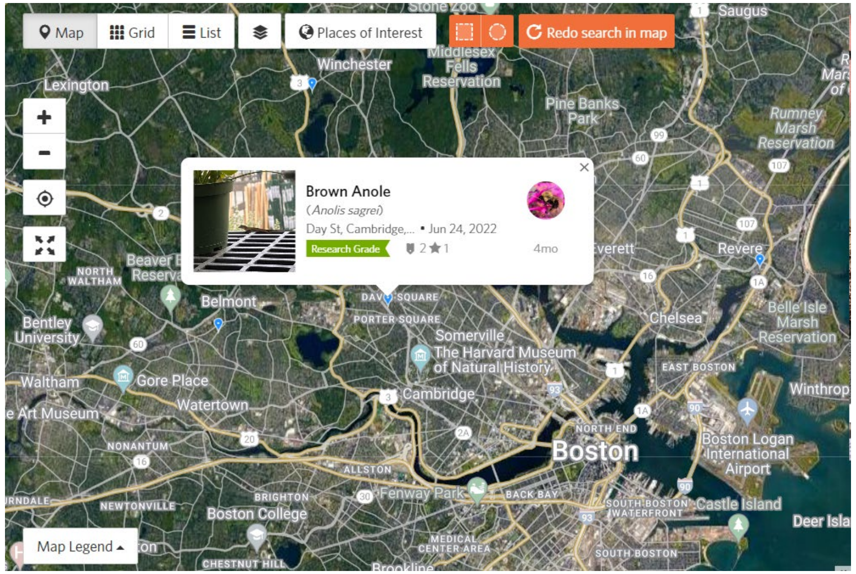



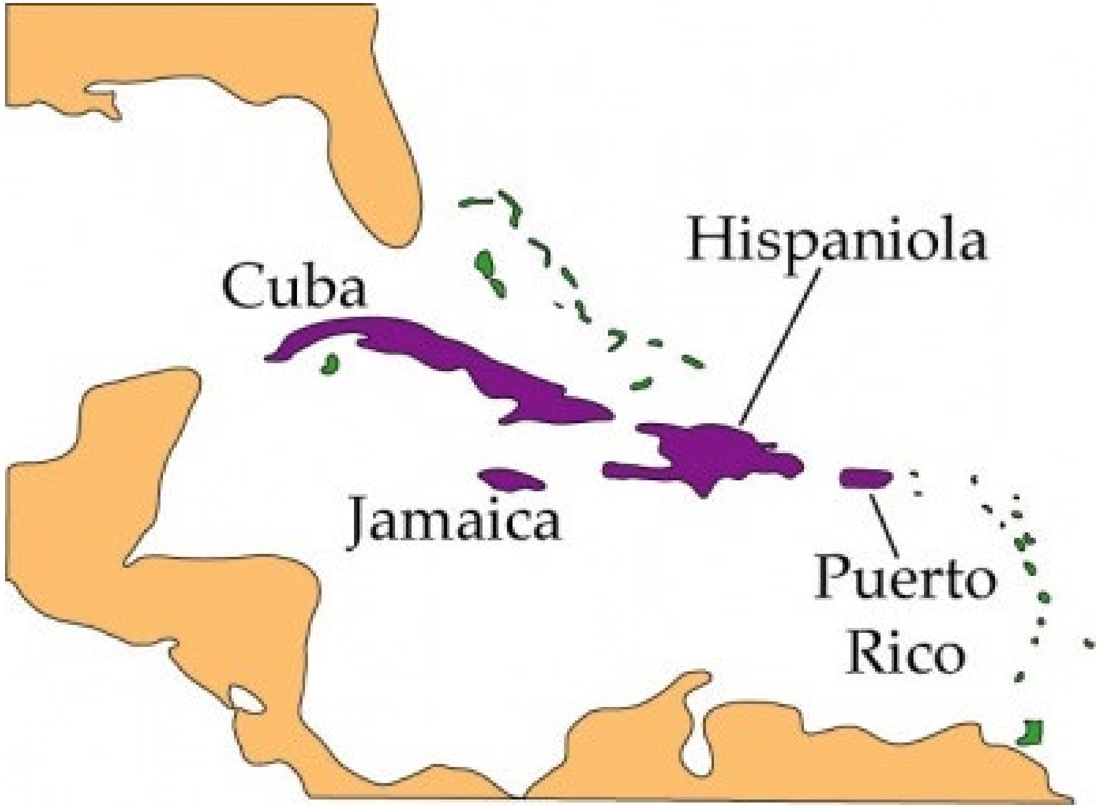

Donihue et al. 2018, Nature

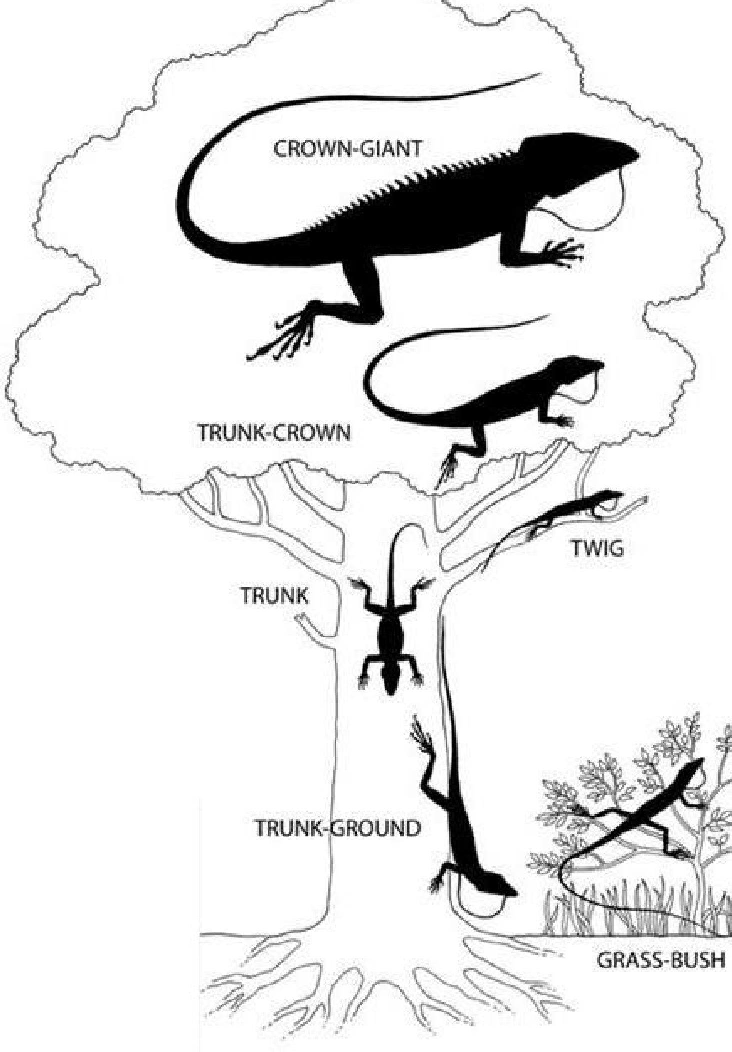
# Geographic distribution of *Anolis*


Canada
United States
Mexico
Cuba
Puerto Rico
Guatemala
Nicaragua
Venezuela
Guyana
Suriname
Colombia
Ecuador
Peru
Brazil
Bolivia
Paraguay
Chile
Uruguay
Argentina
iNaturalist

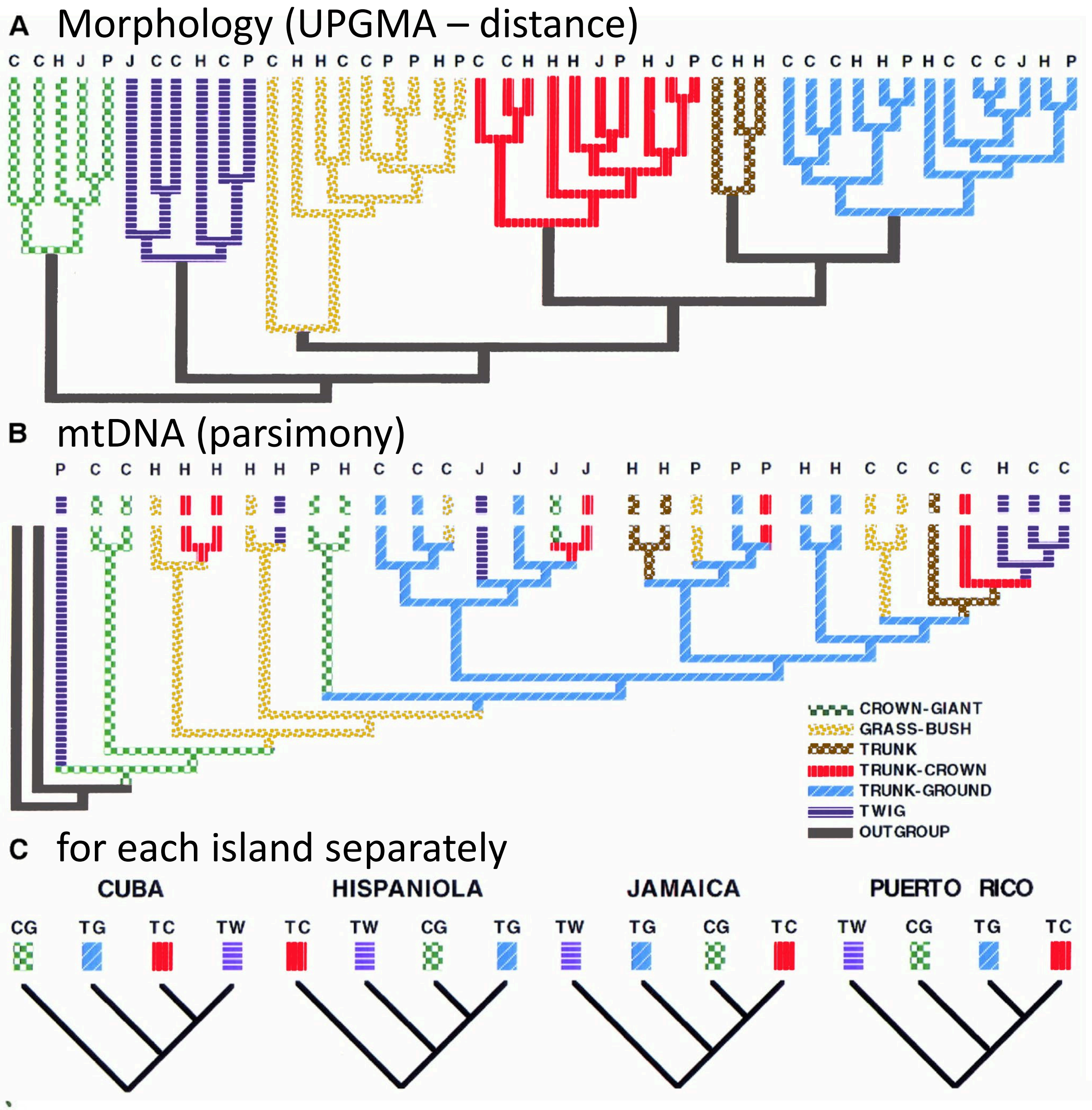

Map
Grid
List
Places of Interest
Redo search in map
ILLINOIS
INDIANA
OHIO
PENNSYLVANIA
Philadelphia
New York
St. Louis
Indianapolis
KANSAS
MISSOURI
WEST VIRGINIA
Washington
KENTUCKY
VIRGINIA
Nashville
OKLAHOMA
ARKANSAS
MISSISSIPPI
ALABAMA
GEORGIA
TEXAS
Jacksonville
San Antonio
COAHUILA
NUEVO LEON
Monterrey
Gulf of Mexico
Havana
The Bahamas
Map Legend

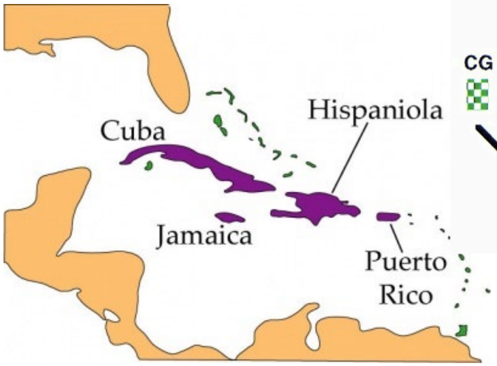

Map
Grid
List
Places of Interest
Redo search in map
Lexington
Winchester
Middlesex Fells Reservation
Pine Banks Park
Saugus
Brown Anole
(Anolis sagrei)
Day St, Cambridge,...
Jun 24, 2022
Research Grade
4mo
Belmont
Bentley University
Somerville
The Harvard Museum of Natural History
Waltham
Gore Place
Watertown
Cambridge
Chelsea
Revere
Winthrop
Boston
Boston Logan International Airport
Fenway Park
Boston College
Castle Island
Map Legend

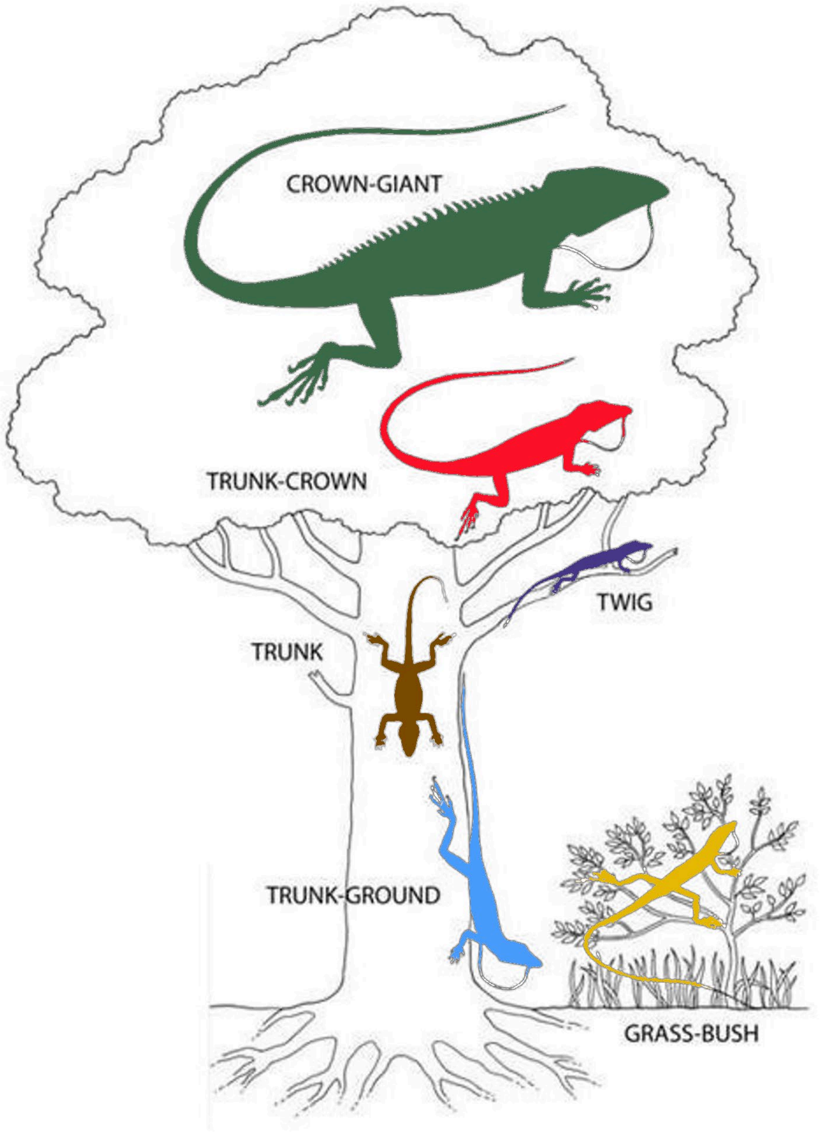

Cuba
Hispaniola
Jamaica
Puerto
Rico


CROWN-GIANT
TRUNK-CROWN
TWIG
TRUNK
TRUNK-GROUND
GRASS-BUSH

# Adaptive radiation of *Anolis* lizards in the Greater Antilles




Losos et al. 1998

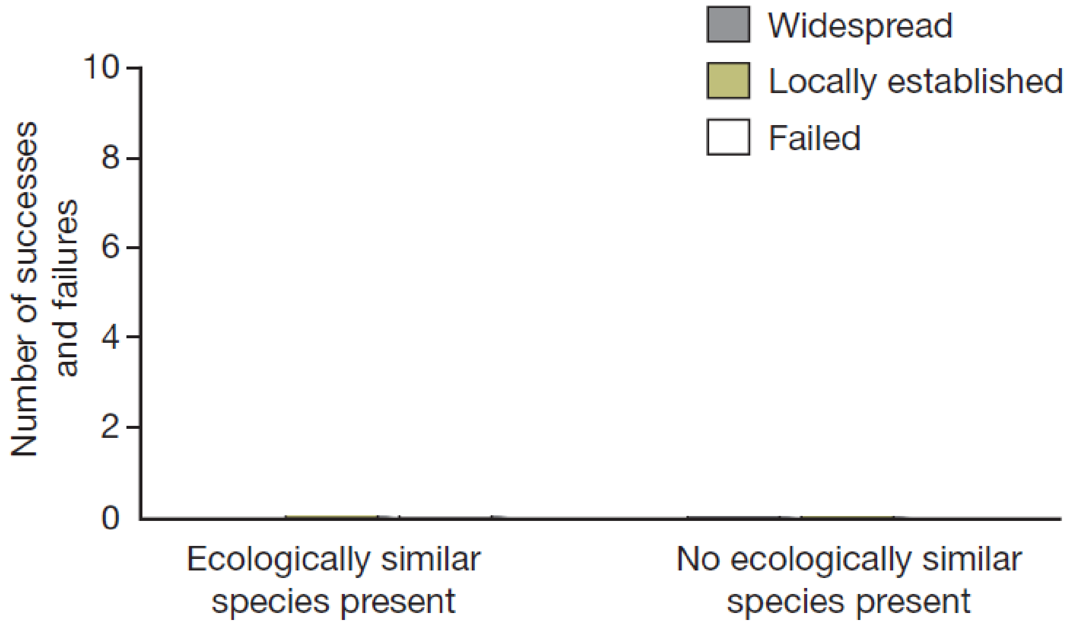
The hypothesis of resource competition as the driver of adaptive radiation makes 3 testable predictions

1) Sympatric species interact ecologically (e.g. through competition)
2) Consequently, species alter their resource use
3) And then evolve appropriate adaptations.

# Resource competition hypothesis

## Prediction 1: Sympatric species interact ecologically

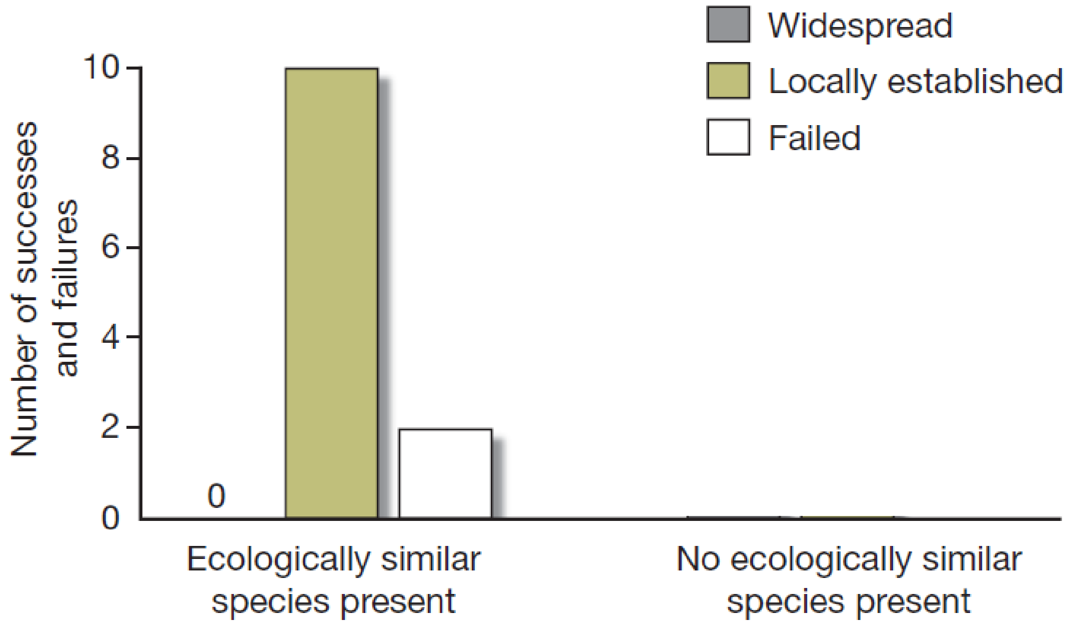
Evidence from introductions



# Resource competition hypothesis

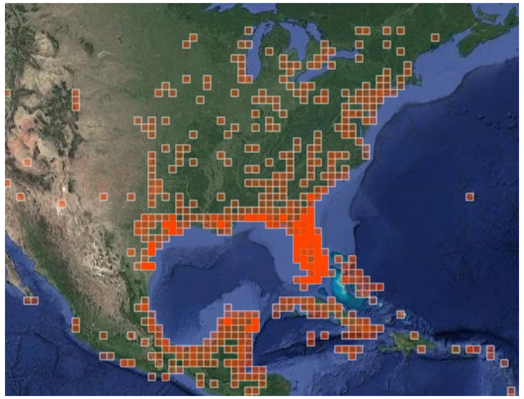
## Prediction 1: Sympatric species interact ecologically

Evidence from introductions




The priority effect

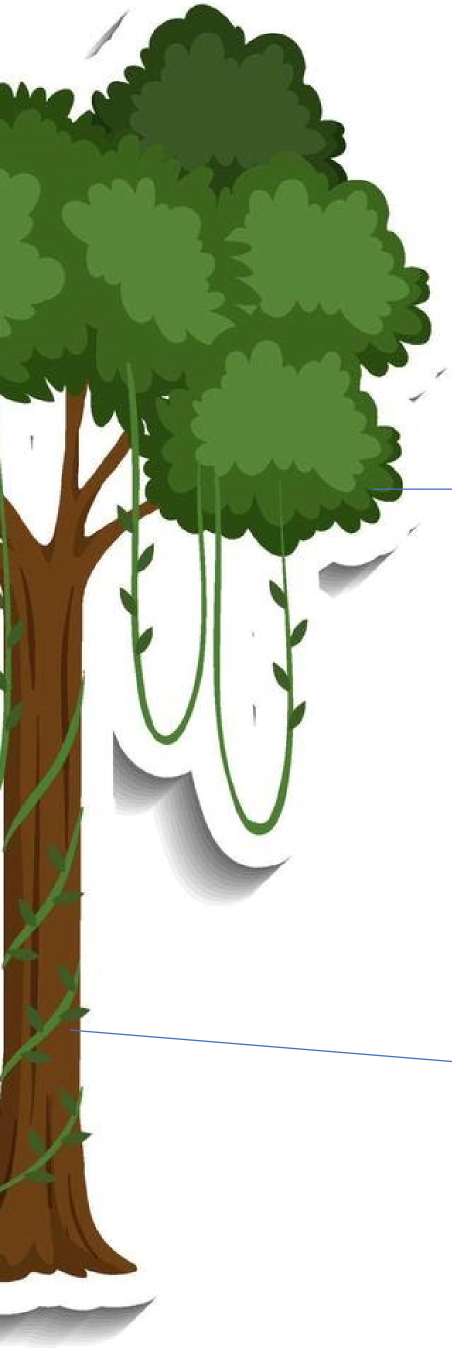
*Anolis sagrei*
(the Cuban Brown Anole,
a "trunk-ground" ecomorph)



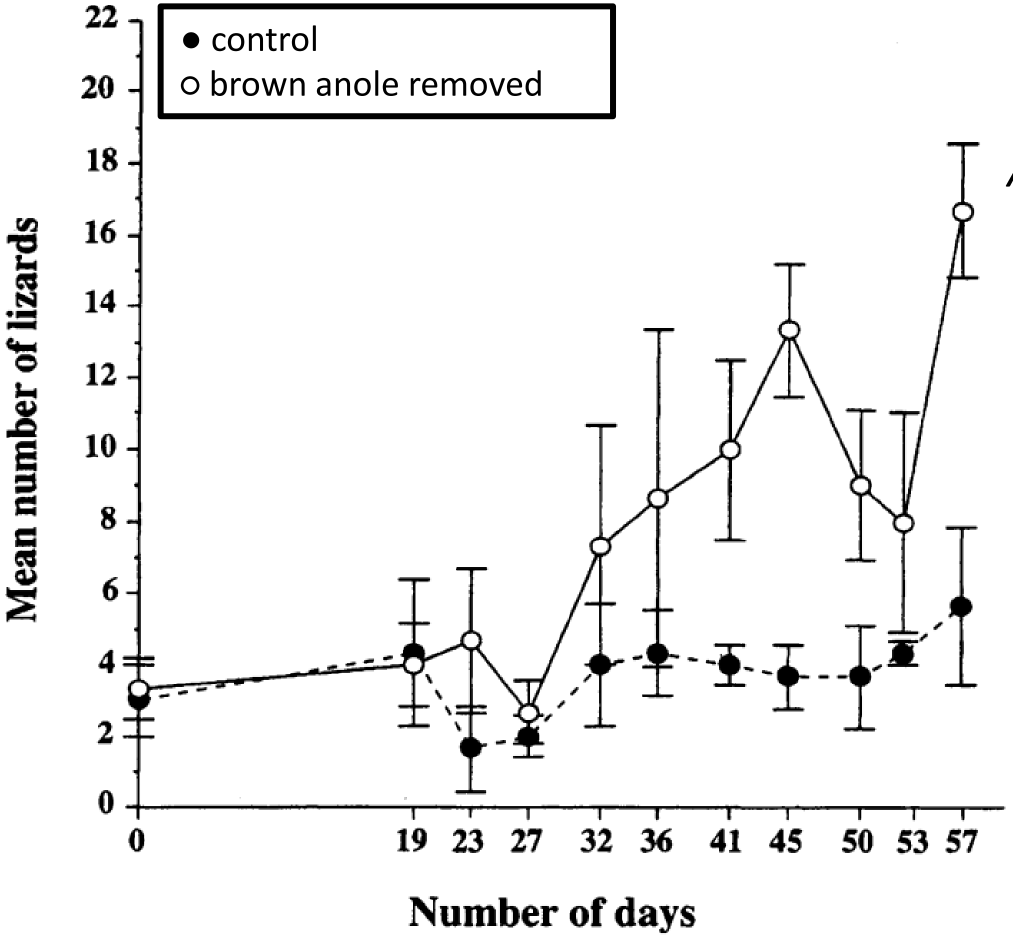
Losos et al. 1993

# Prediction 1: Sympatric species interact ecologically

## Experimental evidence



*Introduction of Anolis evermannii*
green "trunk-crown" ecomorph)




*Anolis gundlachi*
absent

*Anolis gundlachi,*
a brown "trunk-ground" ecomorph,
present

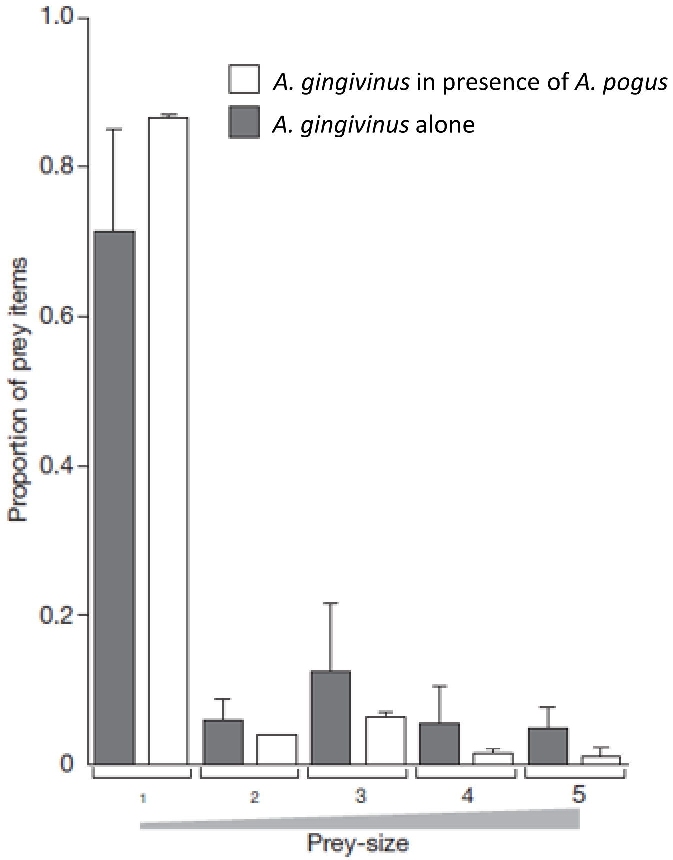
Leal et al. 1998

The hypothesis of resource competition as the driver of adaptive radiation makes 3 testable predictions

1) Sympatric species interact ecologically (e.g. through competition)
2) **Consequently, species alter their resource use**
3) And then evolve appropriate adaptations.

# Prediction 2: species alter their resource use

## <u>Experimental evidence</u>




*A. gingivinus*

*A. pogus*

TABLE 9. Perch heights of *Anolis gingivinus* and *A. bimaculatus* in each enclosure.

| Species | Enclosure* | Perch height (m) $\bar{x}$ | Perch height (m) SD | No. observations |
|---|---|---|---|---|
| *A. gingivinus* | GW1 | 0.89 | 0.81 | 235 |
| | GW2 | 0.87 | 0.79 | 205 |
| | G1 | 0.38 | 0.18 | 242 |
| | G2 | 0.49 | 0.42 | 202 |

↑ presence of *A. pogus* (GW1, GW2)

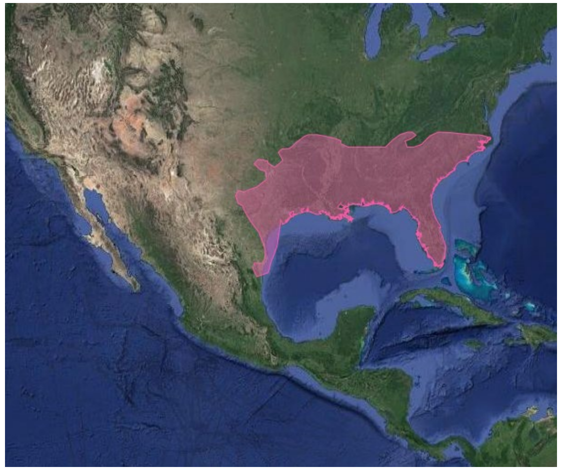
↓ absence of *A. pogus* (G1, G2)

Pacala and Roughgarden 1985

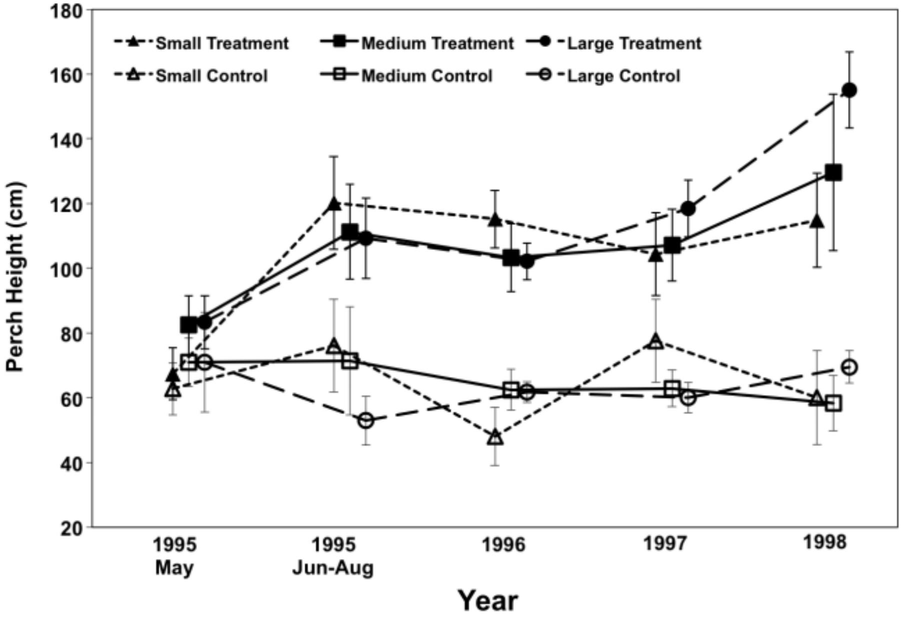
# Prediction 2: species alter their resource use

## Evidence from introductions


Native *Anolis carolinensis*
Normally from ground to crown



*Experiments done on small islands of coast of Florida*




Presence *A. sagrei*

Absence *A. sagrei*

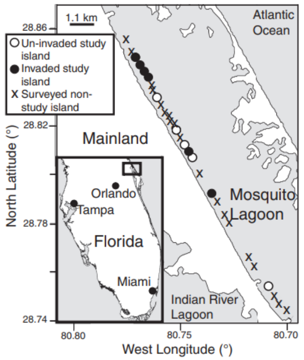
Invasive *Anolis sagrei*
(the Cuban Brown Anole,
a “trunk-ground” ecomorph)

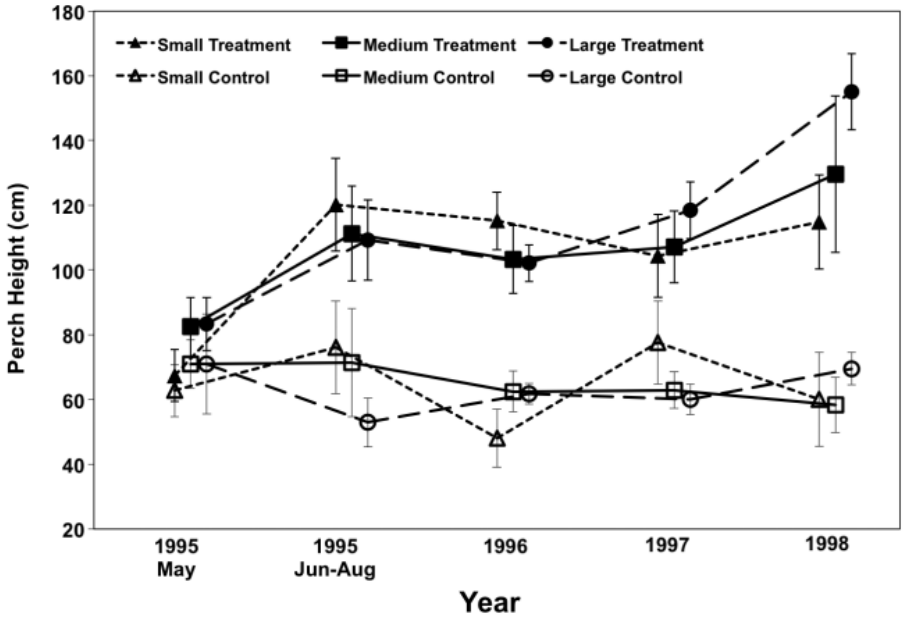
Campbell 2000
Stuart et al. 2014

The hypothesis of resource competition as the driver of adaptive radiation makes 3 testable predictions

1) Sympatric species interact ecologically (e.g. through competition)
2) Consequently, species alter their resource use
3) **And then evolve appropriate adaptations.**

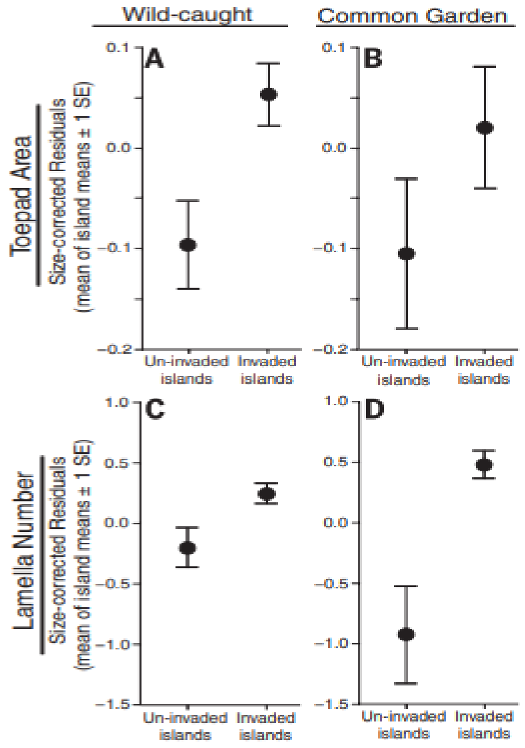
# Prediction 3: Species evolve appropriate adaptations.

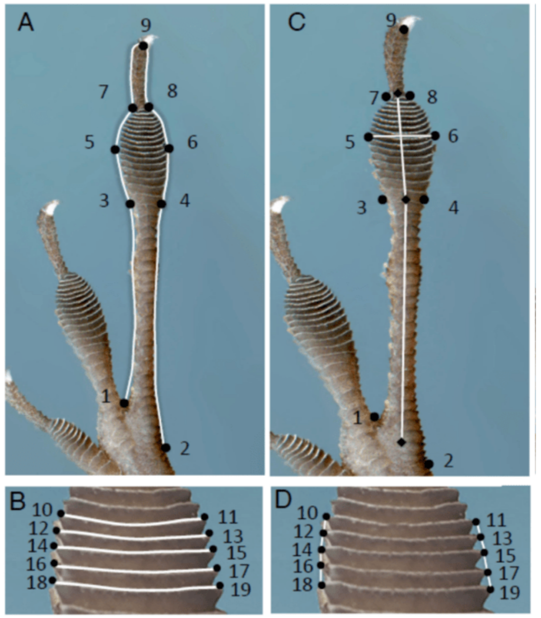


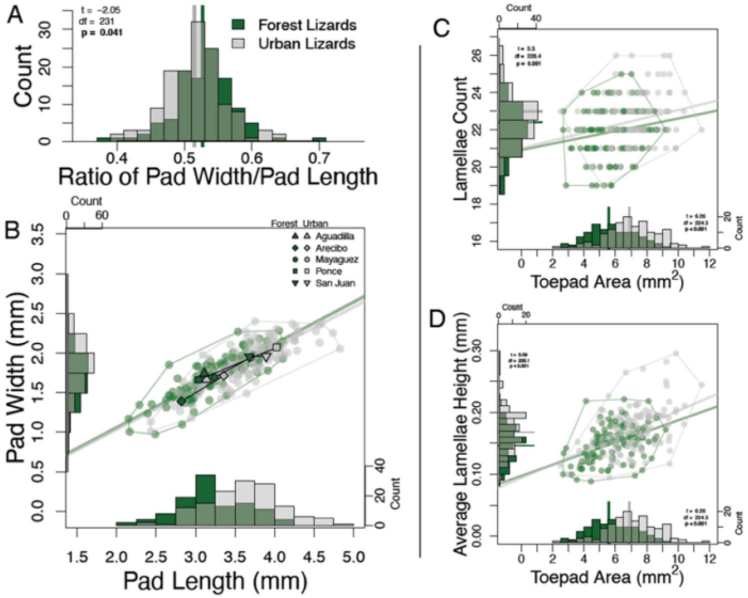

Presence
*A. sagrei*

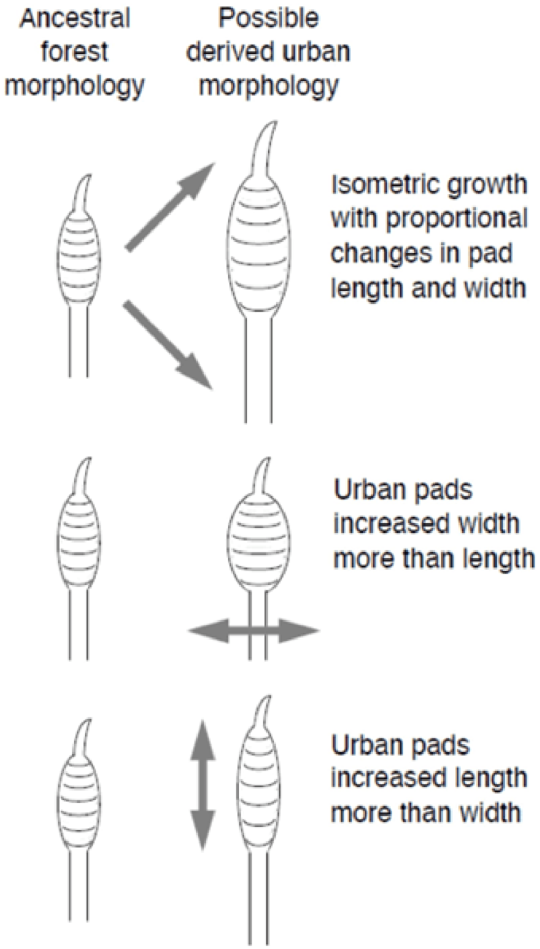
Absence
*A. sagrei*




Stuart et al. 2014




Howell et al. (2022).

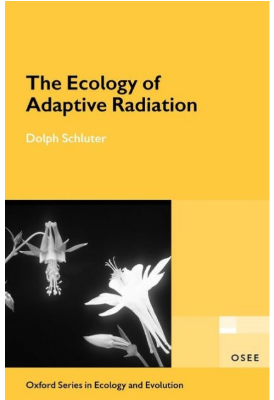
Resource competition seems a reasonable explanation for adaptive radiation in *Anolis*

1) Sympatric species interact ecologically (e.g. through competition)
2) Consequently, species alter their resource use
3) And then evolve appropriate adaptations.

# Adaptive radiations – wrinkles

# Adaptive radiations – wrinkles

Adaptive radiation is the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage.




Schluter 2001

Adaptive radiations have 3 major characteristics:

1) Multiplication of species from a common ancestor
2) Adaptation through natural selection
3) Extraordinary diversification

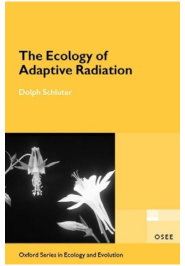
Glor 2010

# Adaptive radiations – wrinkles

Rapid speciation is not well defined

4 possible criteria

- Periods of time within a clade in which branching rates exceed those before and/or later
- Asymmetries between sister clades in number of species
- Periods of time or lineages where speciation exceeds extinction
- Periods of time or lineages where reproductive isolation evolves "unusually" rapidly

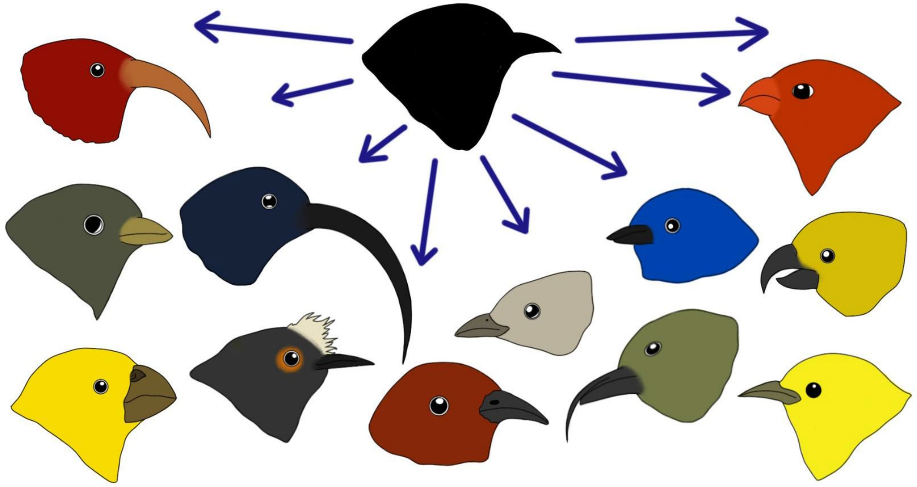



Schluter 2001

# Adaptive radiations – wrinkles

**The important aspect of adaptive radiation is the extent of ecological disparity exhibited by a clade**; whether this disparity arises rapidly or gradually is an empirical question to be tested, not subsumed in the definition.

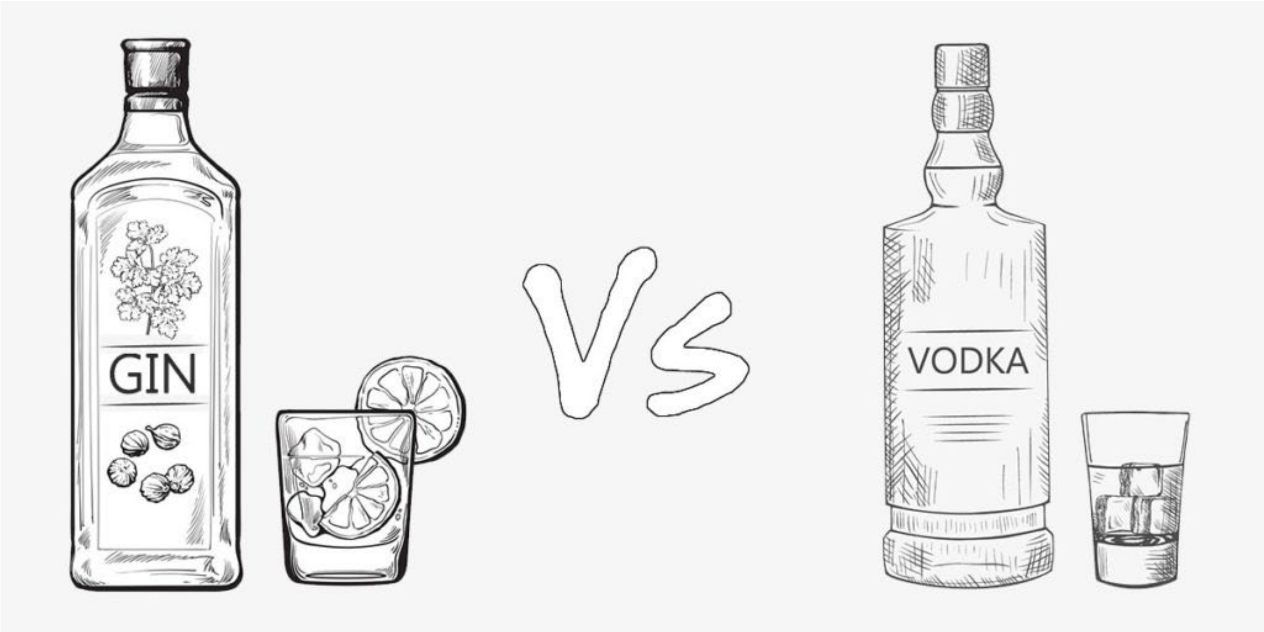
Givnish 1997



“Adaptive radiation is what happened on Earth over the past four billion years.

But this view is so broad that it converts a useful concept into a truism, as airy and dizzying as vodka. I recommend the narrow view, which is focused and pungent, like gin.”

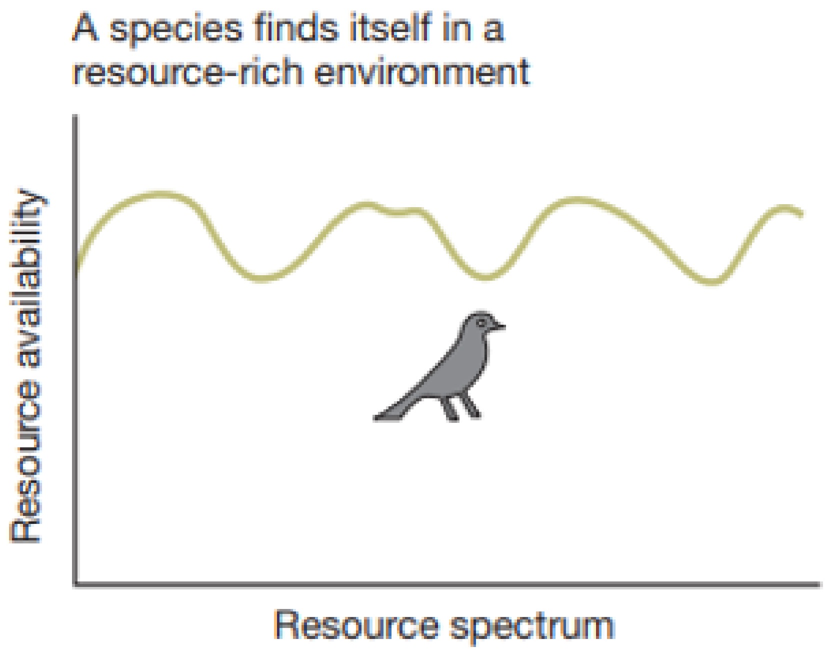
Quammon, 1996.



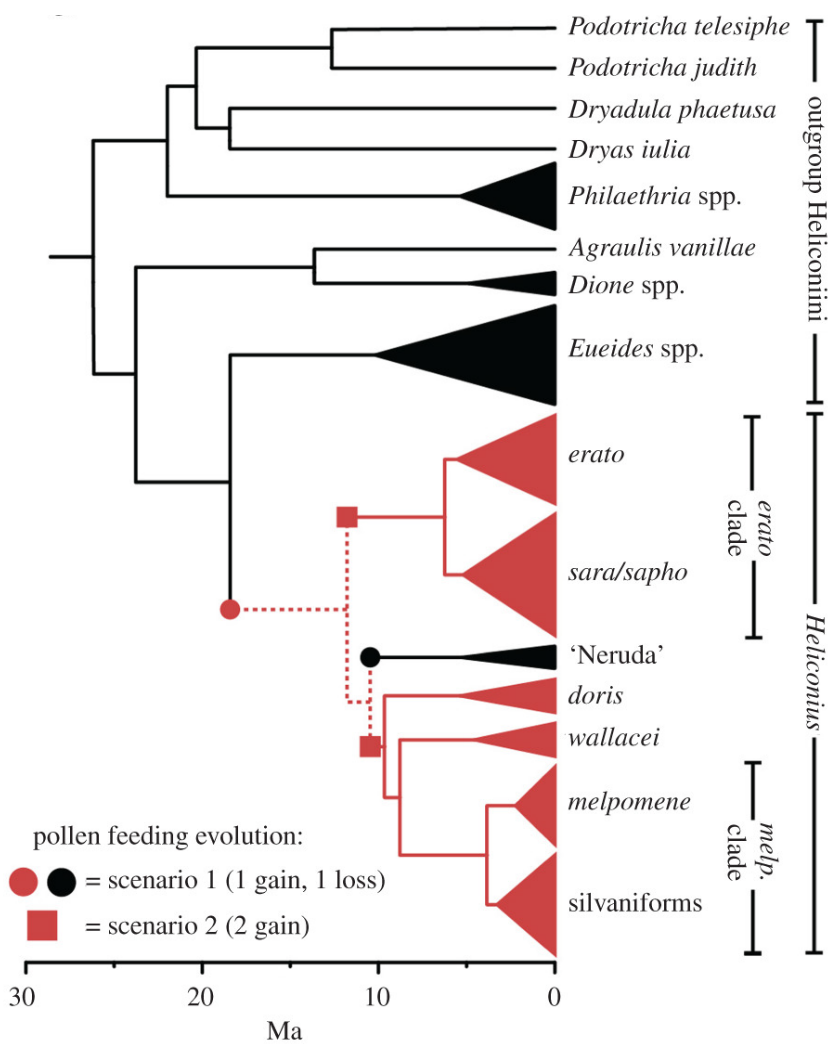
# Adaptive radiations – wrinkles

- **Key innovation**

A trait that allows a species to interact with the environment in novel ways, placing it in a resource-rich environment, and providing the conditions for adaptive radiation.



# Pollen feeding in Heliconius – a “key innovation”?



# Adaptive radiations – wrinkles

- What is a non-adaptive radiation, anyway?

Non-adaptive radiation is rapid proliferation of species accompanied by negligible or infrequent ecological differentiation, or phenotypic differentiation unrelated to the environment.

Gittenberger, 1991.

Brooks et al. 1985.

- *Albinaria* land snails from Greece
- 75 species
- Wide variety of shell forms, but are apparently indistinguishable by environment.
- But maybe researchers have missed something important?


According to Schluter (2000):

“Non-adaptive radiation is a logical null-hypothesis”

# Speciation and adaptive radiations

*Either*

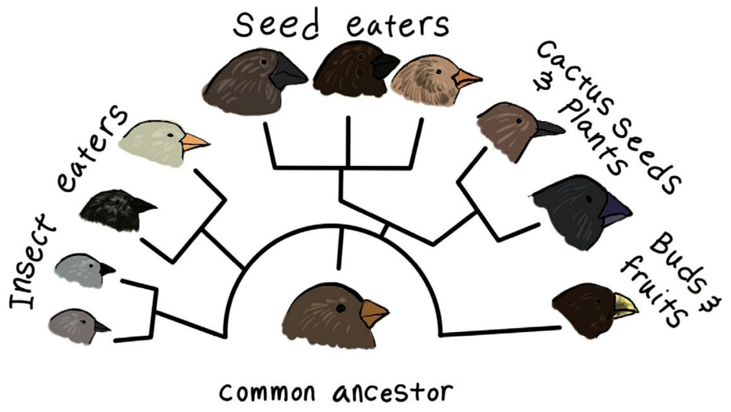
Allopatric speciation

↓

Species come into secondary contact

↓

Phenotypic divergence due to competition




*Or..*

Speciation happens **as a consequence of** ecological divergence (speciation and phenotypic differentiation happen simultaneously).

= Ecological Speciation

Ecological speciation is the process by which barriers to gene flow evolve between populations as a result of ecologically based, divergent selection between environments.

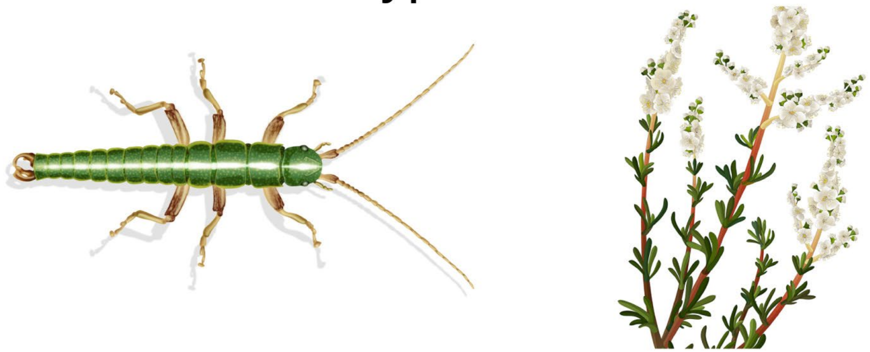
In other words, do phenotypic and species diversity arise via the same process?

Darwin thought somewhat along these lines*, but the idea was side-lined until the late 1990s

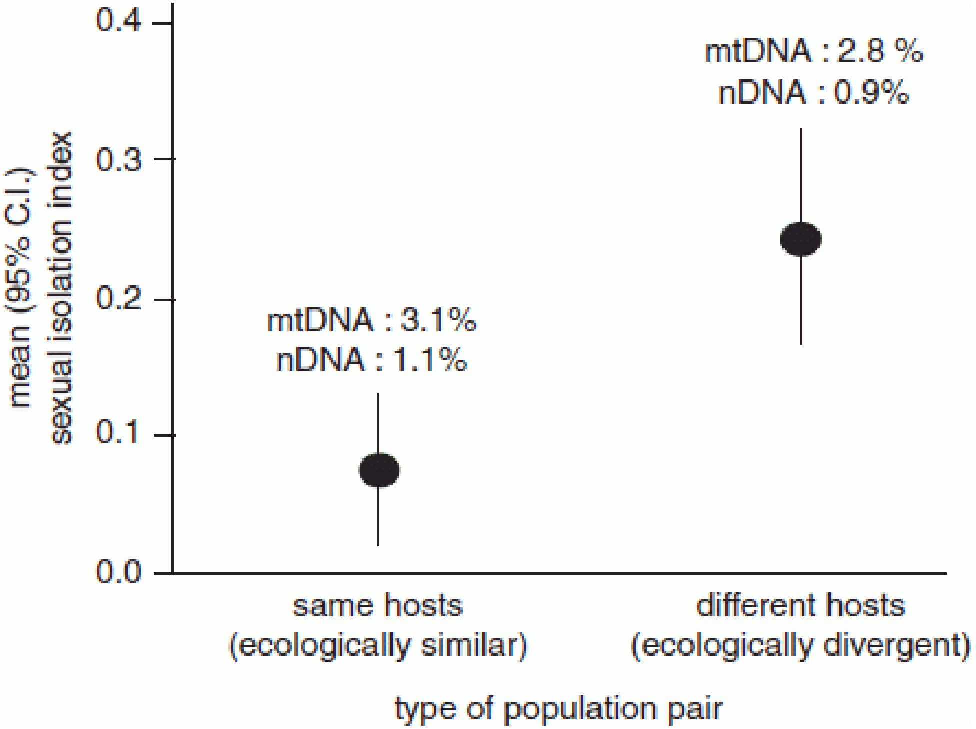
*but I may disagree here; I think Darwin could be referring to the persistence of species after forming somehow

# Prediction: genetic divergence ~ ecological difference

*Adenostoma* ecotype



*Ceanothus* ecotype

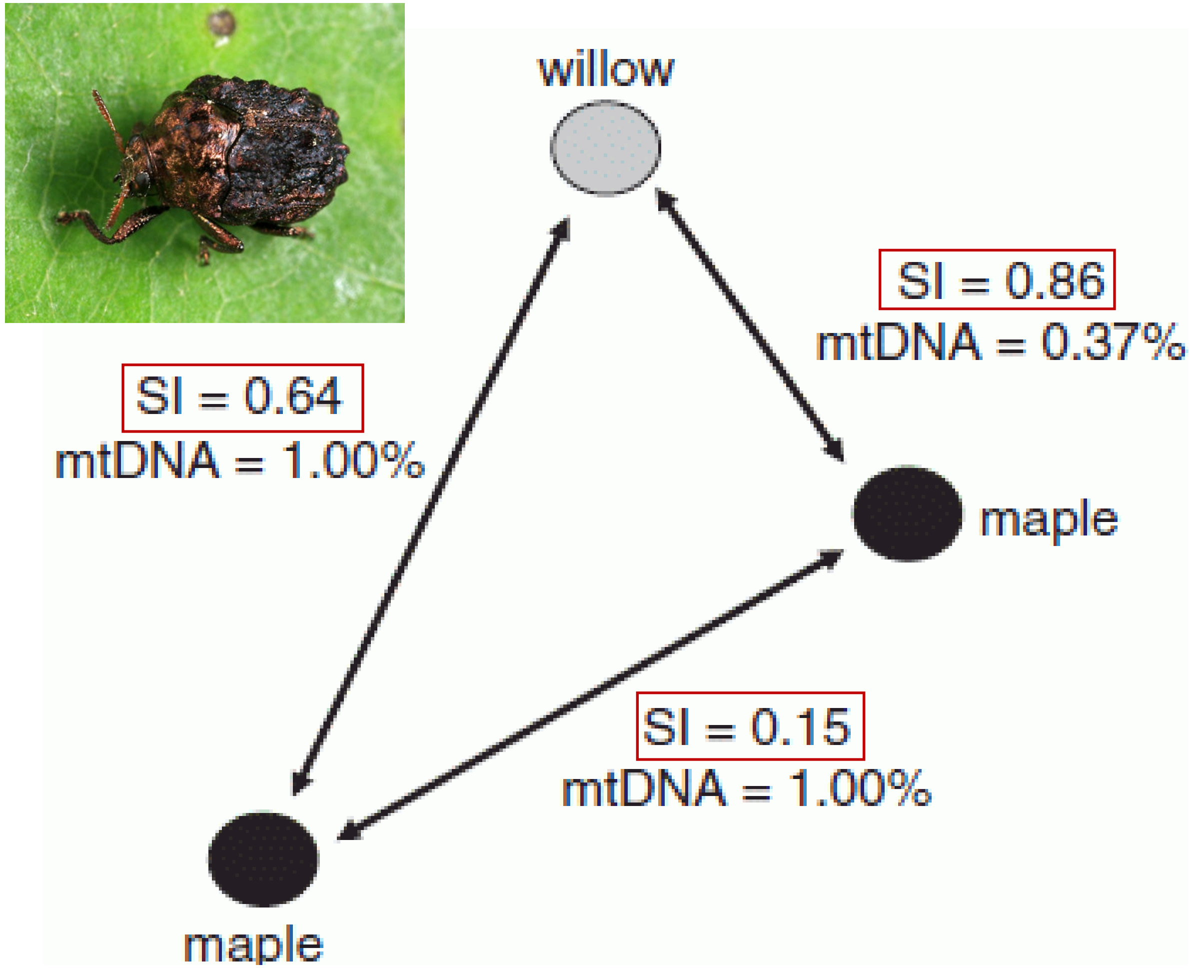



*Timema cristinae* walking stick insects

Nosil et al. 2002

# Prediction: reproductive isolation ~ ecological difference

*Neochlamisus bebbinae*



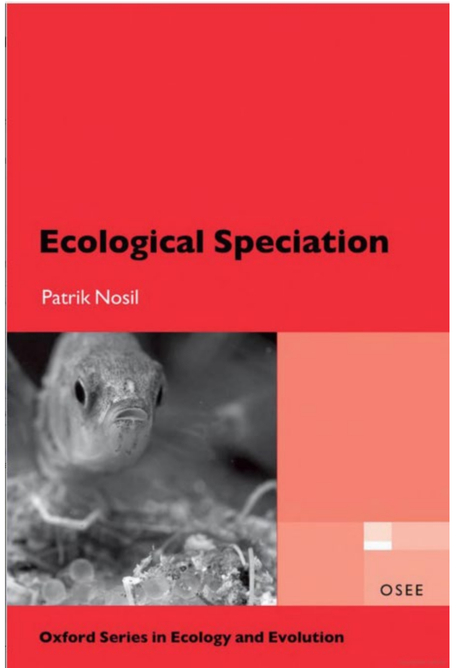

SI = sexual isolation
i.e. assortative mating

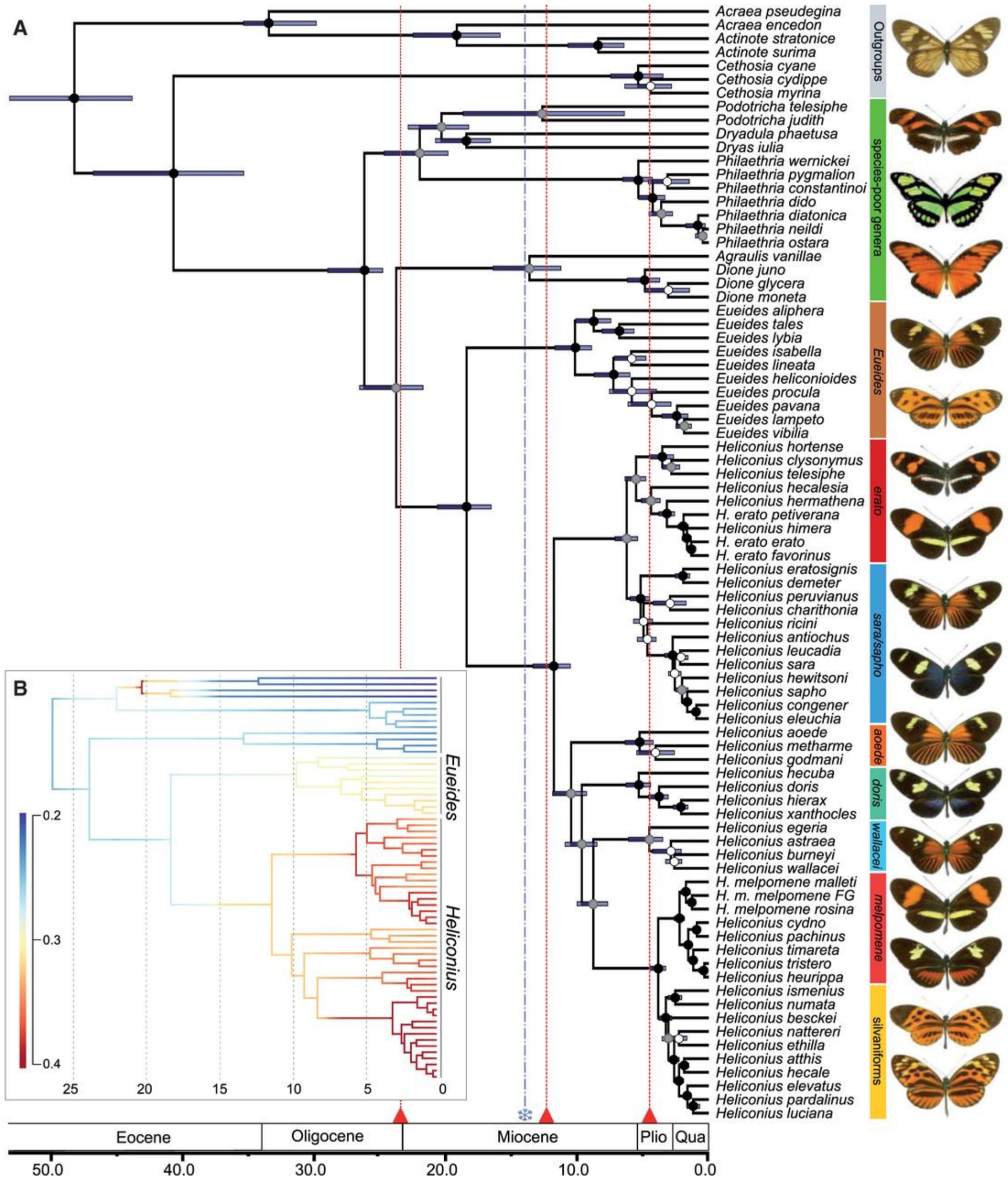
Funk (1998)

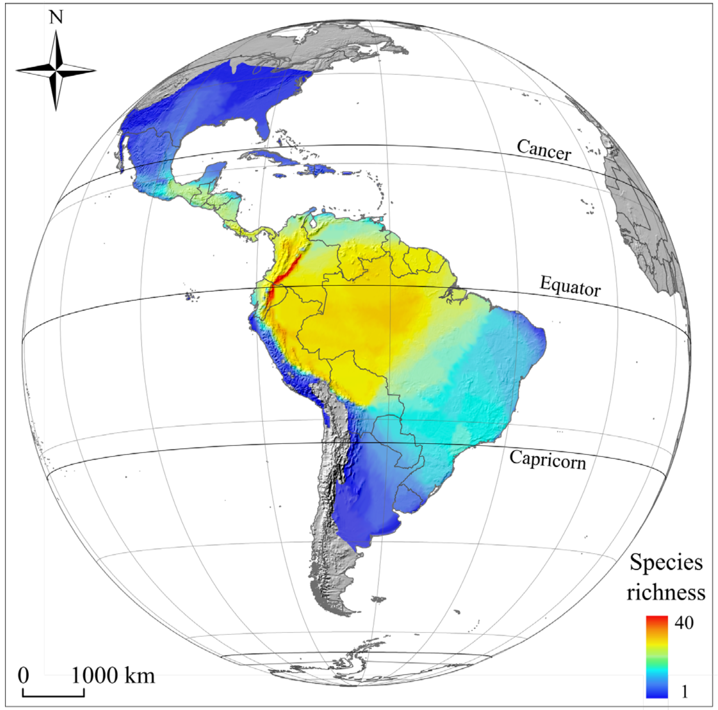
# Ecological speciation has 3 necessary components

1) A source of divergent selection
2) A form of reproductive isolation
3) A genetic mechanism linking selection to RI (pleiotropy or LD).

(essentially, making it nearly a “magic trait”)






Heliconius ~50 species, 350+ subspecies

Aposematic and mimetic

Feed on Passiflora (Passion vines)

# Ecological speciation has 3 necessary components

1) **A source of divergent selection**
2) A form of reproductive isolation
3) A genetic mechanism linking selection to RI (pleiotropy or LD).

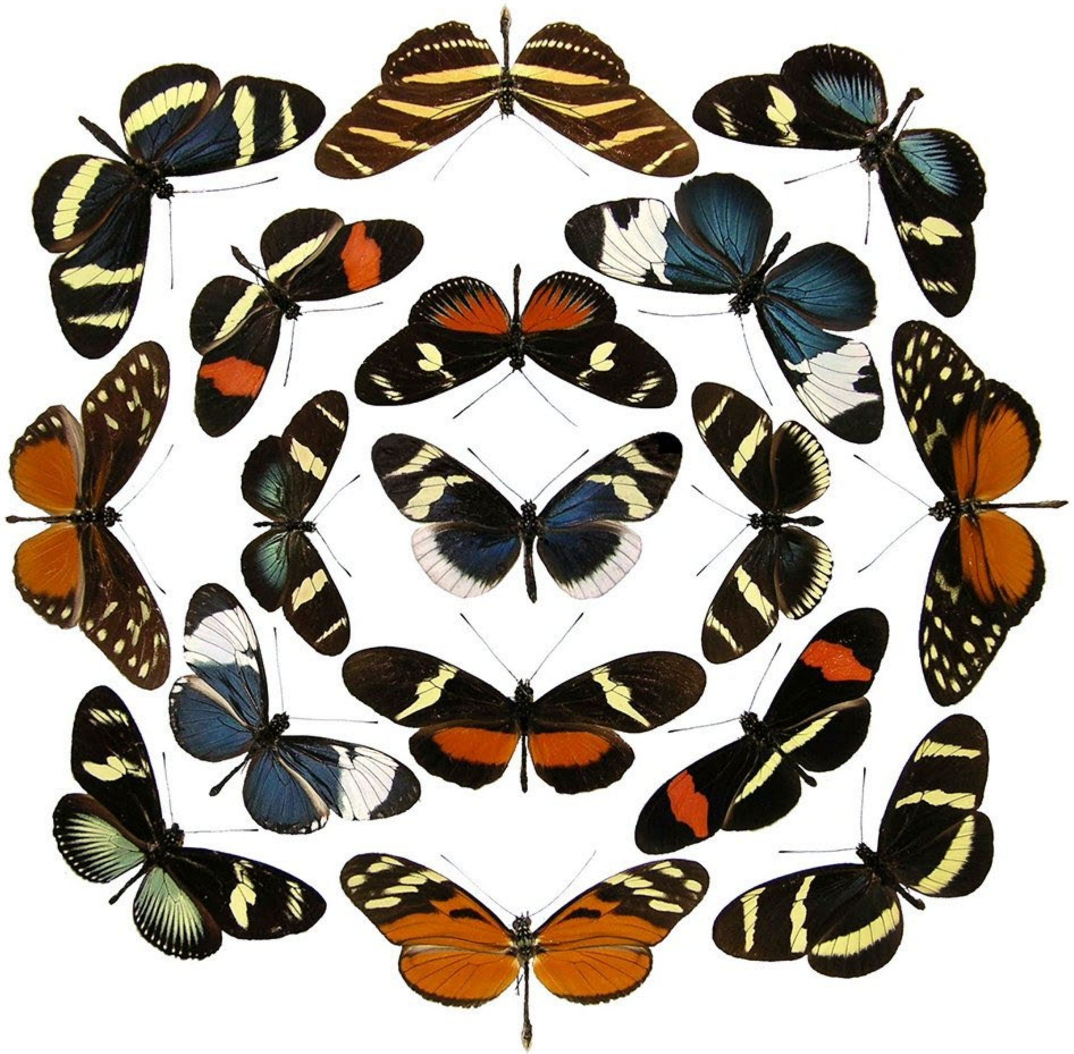
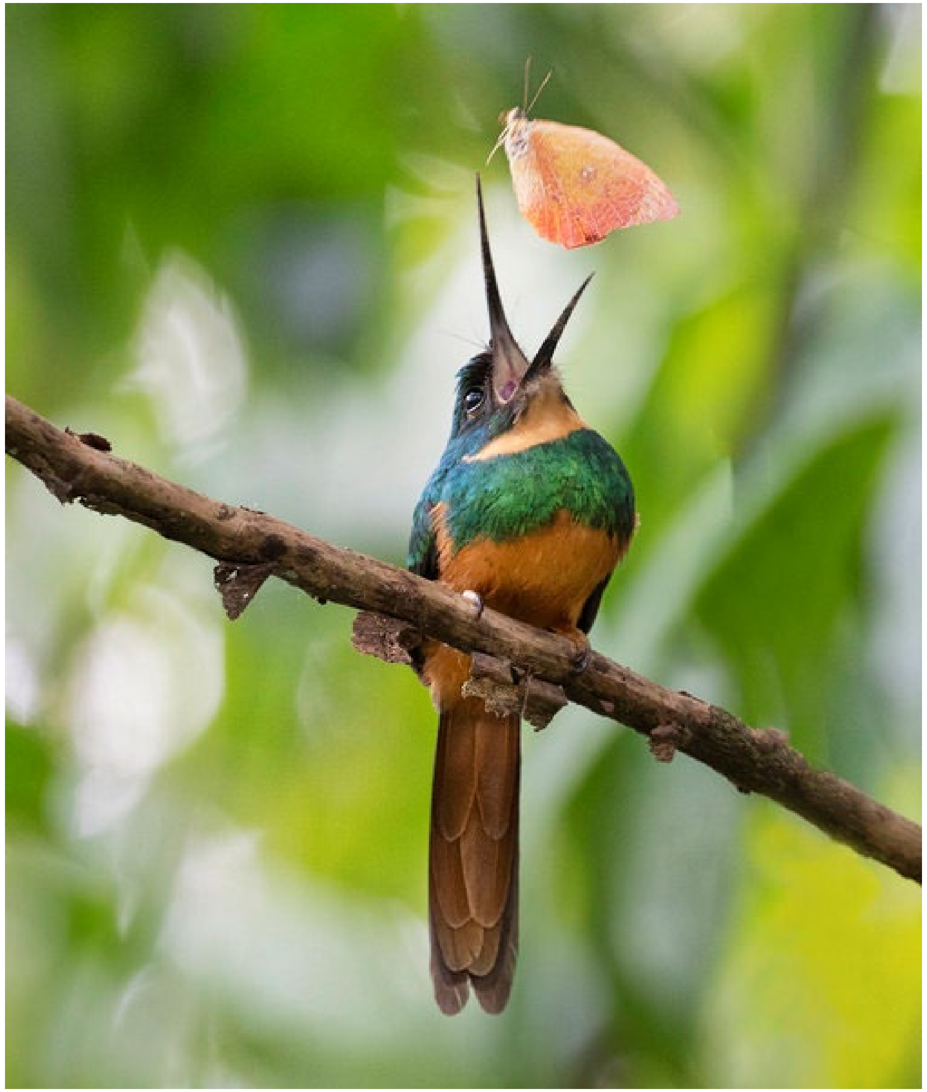


PHOTO: MARCUS KRONFORST/HARVARD UNIVERSITY



**PROCEEDINGS B**

rspb.royalsocietypublishing.org

Research

**Cite this article:** Arias M, le Poul Y, Chouteau M, Boisseau R, Rosser N, Théry M, Llaurens V. 2016 Crossing fitness valleys: empirical estimation of a fitness landscape associated with polymorphic mimicry. *Proc. R. Soc. B* **283**: 20160391.
http://dx.doi.org/10.1098/rspb.2016.0391

Received: 22 February 2016
Accepted: 5 April 2016

**Subject Areas:**
evolution, behaviour, cognition

**Keywords:**
passion-vine butterfly, aposematism, dominance, linkage disequilibrium, generalization, heterozygote

**Author for correspondence:**
Mónica Arias
e-mail: moarias@gmail.com

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2016.0391 or via http://rspb.royalsocietypublishing.org.

THE ROYAL SOCIETY PUBLISHING

# Crossing fitness valleys: empirical estimation of a fitness landscape associated with polymorphic mimicry

Mónica Arias[1,2], Yann le Poul[1], Mathieu Chouteau[1], Romain Boisseau[1,3], Neil Rosser[4], Marc Théry[2] and Violaine Llaurens[1]

[1]Institut Systématique, Evolution, Biodiversité, UMR 7205 MNHN-CNRS-EPHE-UPMC- Sorbonne universités, Muséum National d'Histoire Naturelle, Bâtiment d'entomologie, CP050, 57, rue Cuvier, 75005 Paris, France
[2]UMR CNRS 7179, CNRS-MNHN MECADEV, Muséum National d'Histoire Naturelle, 1, avenue du petit château, 91800 Brunoy, France
[3]Département de Biologie, Ecole Normale supérieure, 75 005 Paris, France
[4]Department of Biology, University of York, Wentworth Way, York YO10 5DD, UK

RB, 0000-0003-4317-1064

Characterizing fitness landscapes associated with polymorphic adaptive traits enables investigation of mechanisms allowing transitions between fitness peaks. Here, we explore how natural selection can promote genetic mechanisms preventing heterozygous phenotypes from falling into non-adaptive valleys. Polymorphic mimicry is an ideal system to investigate such fitness landscapes, because the direction of selection acting on complex mimetic colour patterns can be predicted by the local mimetic community composition. Using more than 5000 artificial butterflies displaying colour patterns exhibited by the polymorphic Müllerian mimic *Heliconius numata*, we directly tested the role of wild predators in shaping fitness landscapes. We compared predation rates on mimetic phenotypes (homozygotes at the supergene controlling colour pattern), intermediate phenotypes (heterozygotes), exotic morphs (absent from the local community) and palatable cryptic phenotypes. Exotic morphs were significantly more attacked than local morphs, highlighting predators' discriminatory capacities. Overall, intermediates were attacked twice as much as local homozygotes, suggesting the existence of deep fitness valleys promoting strict dominance and reduced recombination between supergene alleles. By including information on predators' colour perception, we also showed that protection on intermediates strongly depends on their phenotypic similarity to homozygous phenotypes and that ridges exist between similar phenotypes, which may facilitate divergence in colour patterns.

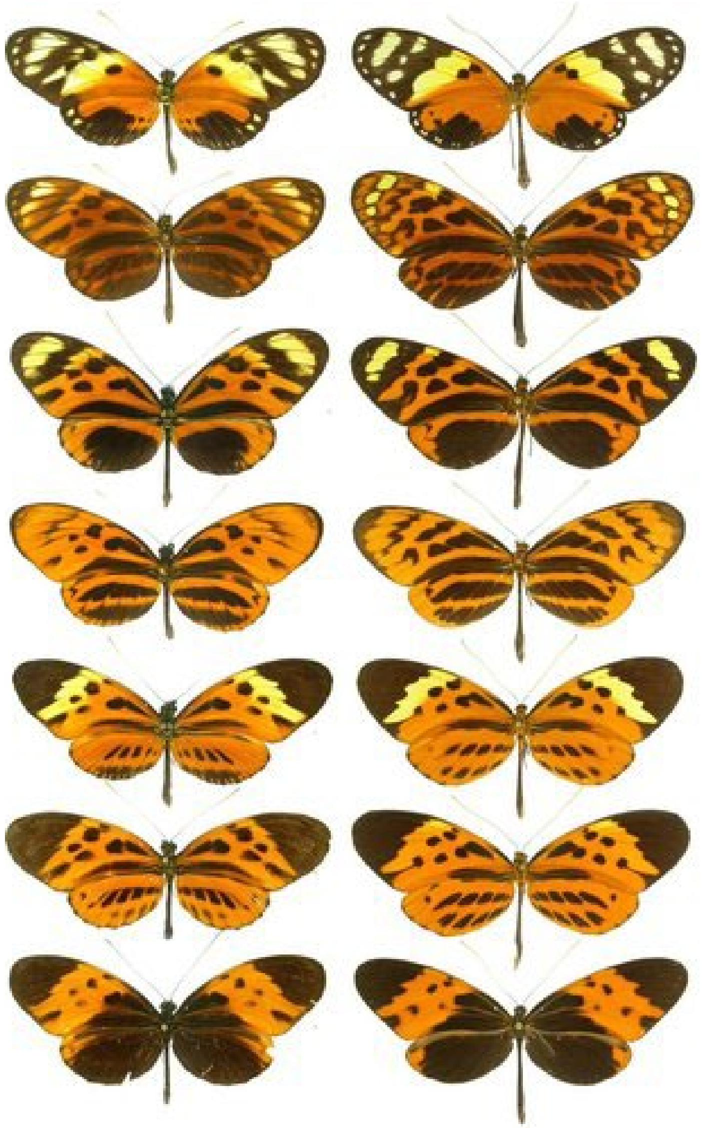
## 1. Background

The origin and persistence of adaptive polymorphisms is a puzzling question for evolutionary biologists [1–4]. Adaptive polymorphisms can be defined as several coexisting phenotypes within a population, which correspond to fitness peaks in an adaptive landscape. Such landscapes may comprise one or many dimensions, depending on the complexity of the adaptive trait. Understanding the evolution of adaptive polymorphism in a complex trait is especially challenging, because natural selection can act on different features of the trait and thus on multiple dimensions of the fitness landscape. Therefore, the exploration of new adaptive peaks in such a landscape usually requires coordinated changes in multiple axes to cross fitness valleys [5]. Gradual changes alone are thought to be generally unable to bridge such fitness valleys [6]. Mechanisms such as epistasis (i.e. when several neutral or deleterious mutations produce fitness benefits when they co-occur) [7] or large size mutation followed by gradual fine-tuning [8] are more likely to allow shifts to new adaptive peaks.

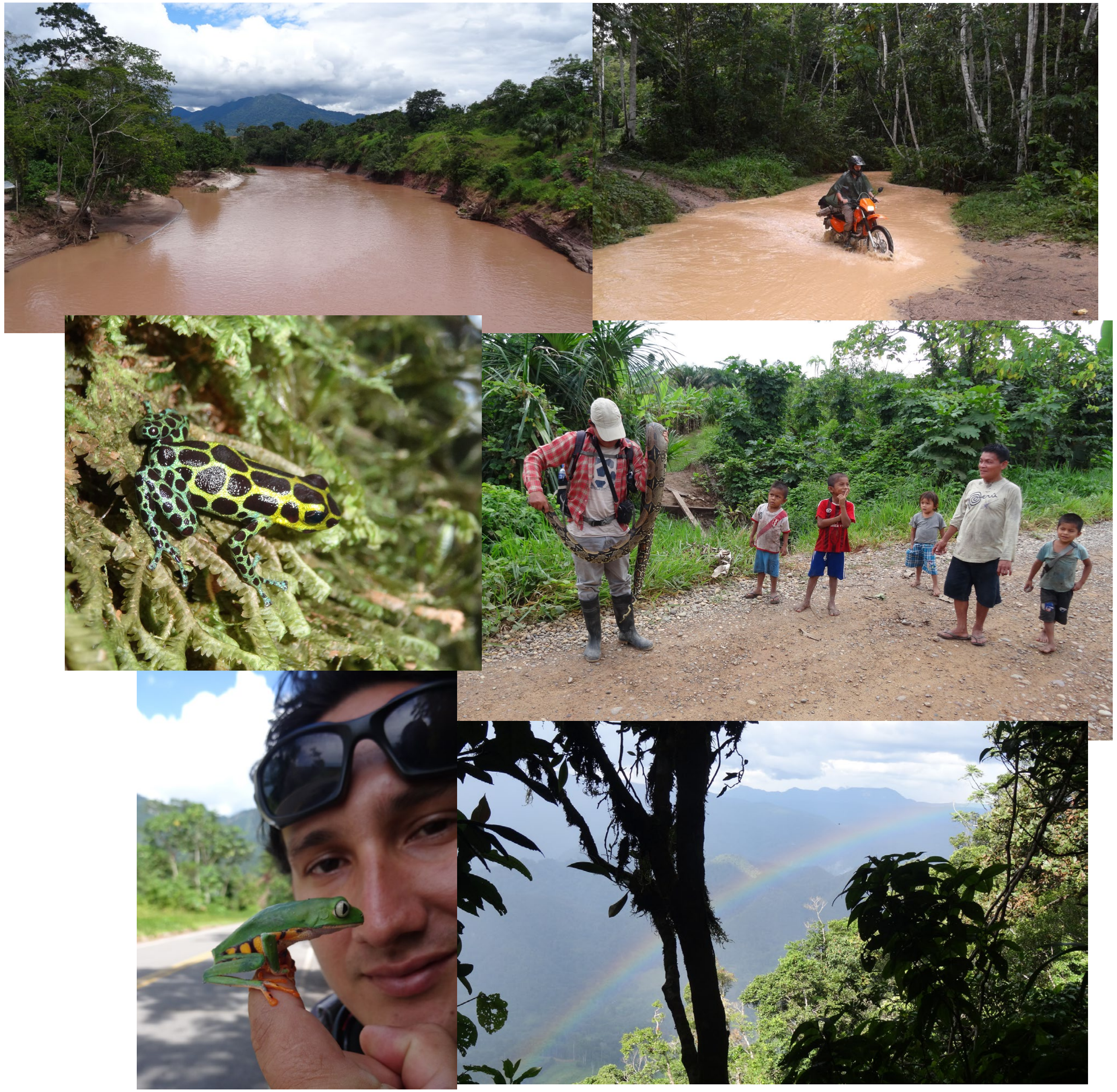


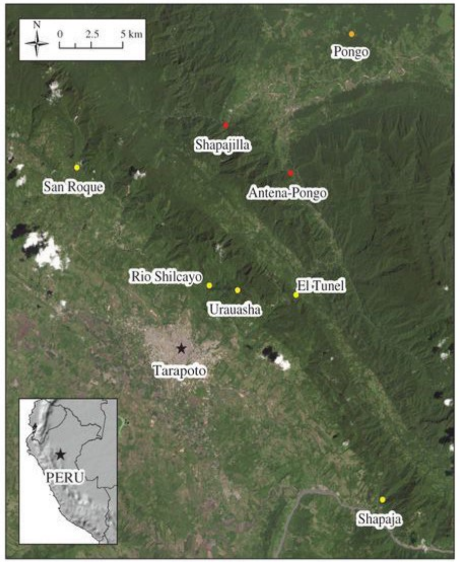
*Heliconius numata* Polymorphic mimic

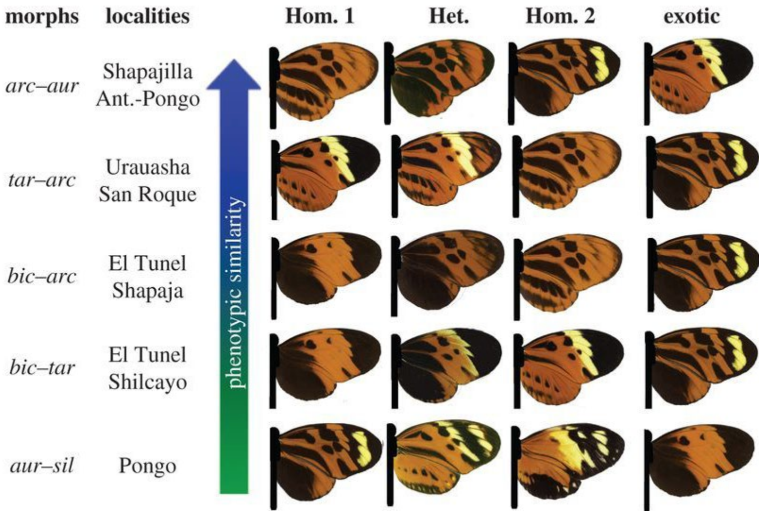
*Melinaea* spp. Models

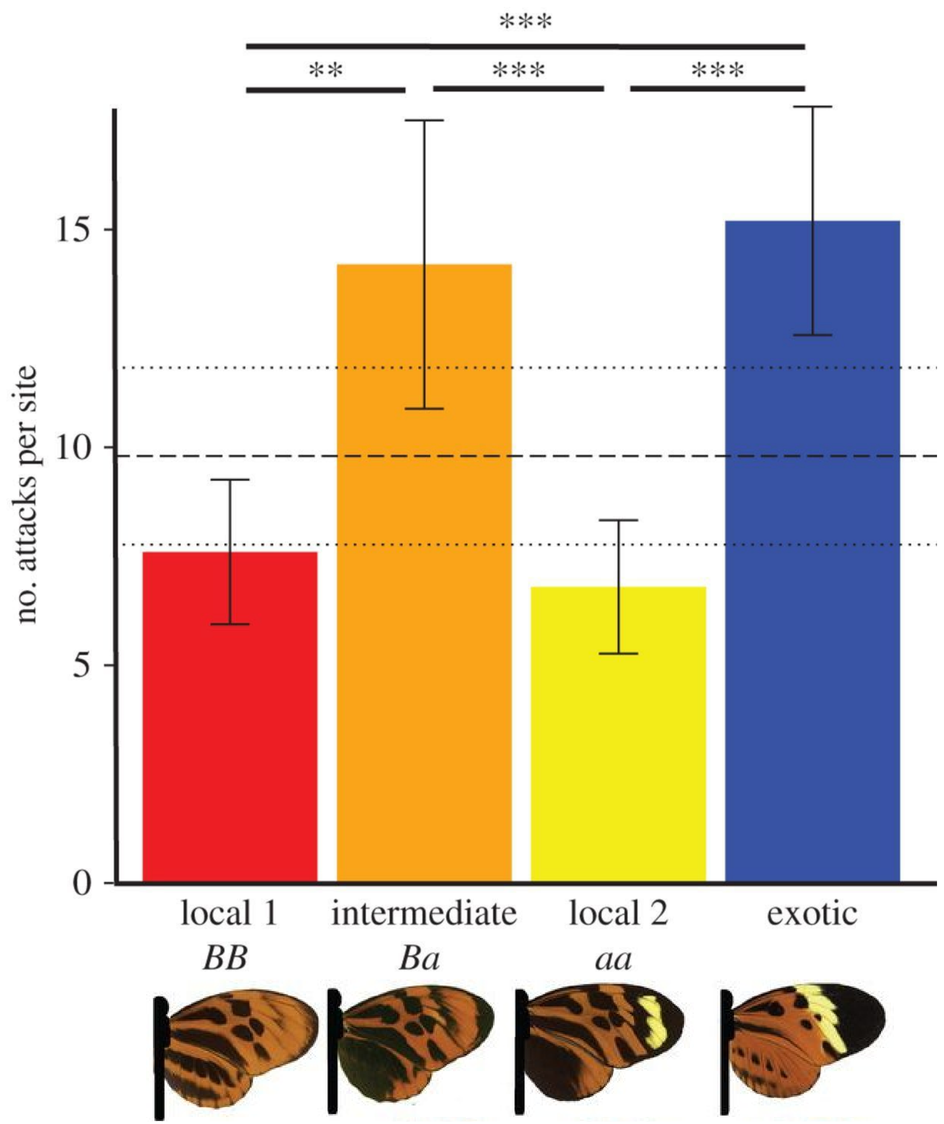



Tarapoto
-5°00'
-10°00'
-15°00'
0
100
200 km
-80°00'
-75°00'
-70°00'

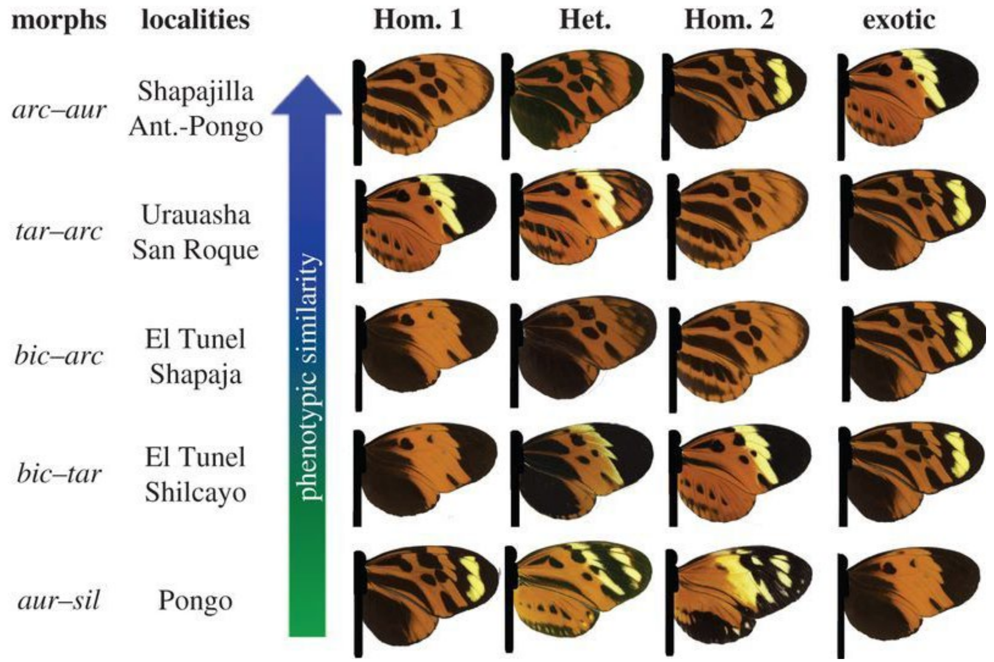



N
0
2.5
5 km
Pongo
Shapajilla
San Roque
Antena-Pongo
Rio Shilcayo
El Tunel
Urauasha
Tarapoto
PERU
Shapaja

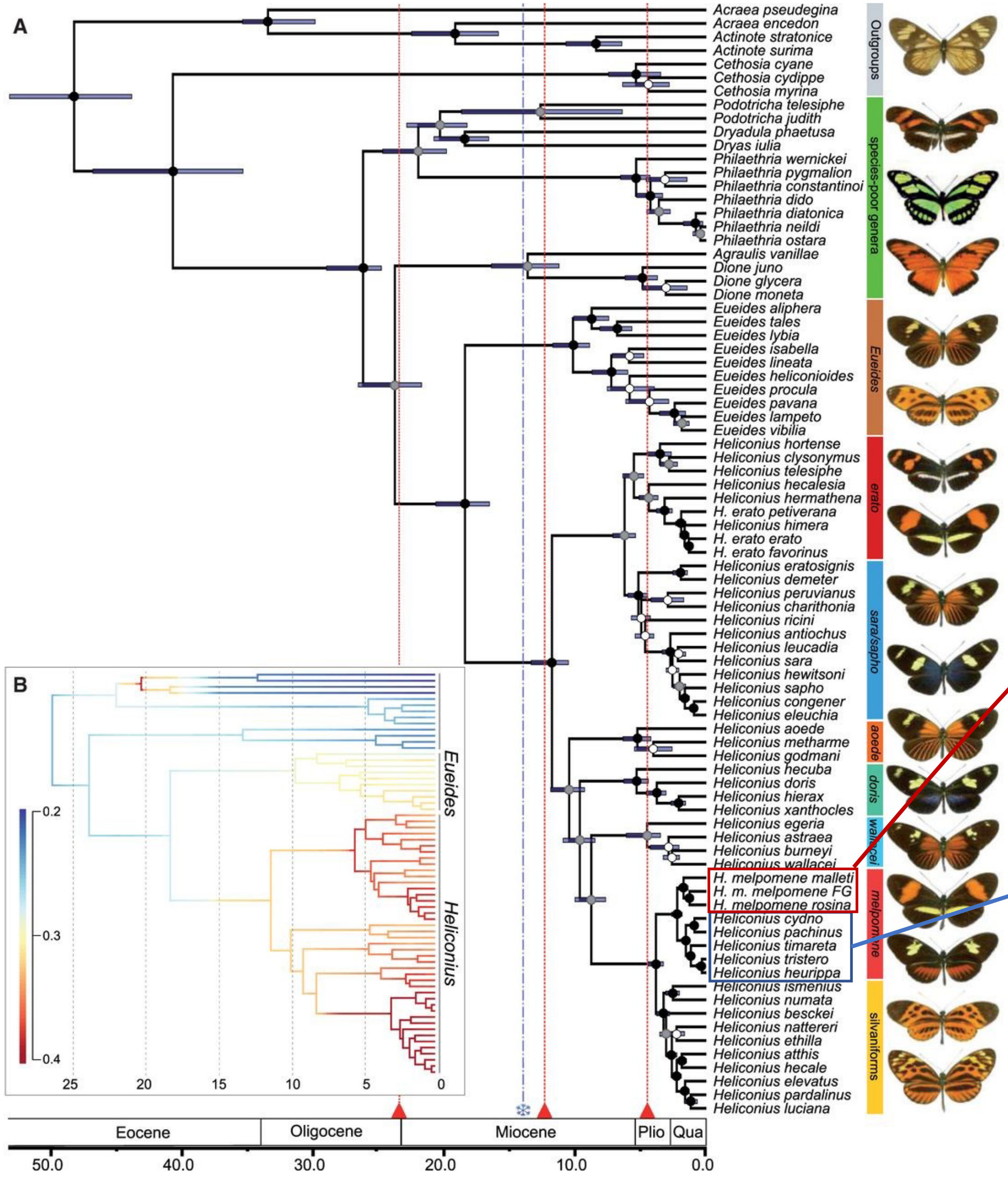

morphs
localities
Hom. 1
Het.
Hom. 2
exotic
arc–aur
Shapajilla
Ant.-Pongo
tar–arc
Urauasha
San Roque
bic–arc
El Tunel
Shapaja
bic–tar
El Tunel
Shilcayo
aur–sil
Pongo
phenotypic similarity



***
**
***
***
no. attacks per site
15
10
5
0
local 1
BB
intermediate
Ba
local 2
aa
exotic

morphs
localities
Hom. 1
Het.
Hom. 2
exotic
arc–aur
Shapajilla
Ant.-Pongo
tar–arc
Urauasha
San Roque
bic–arc
El Tunel
Shapaja
bic–tar
El Tunel
Shilcayo
aur–sil
Pongo
phenotypic similarity




*Heliconius melpomene* and *Heliconius cydno*

Diverged between 1-2 mya

Sympatric in central America and northern SA

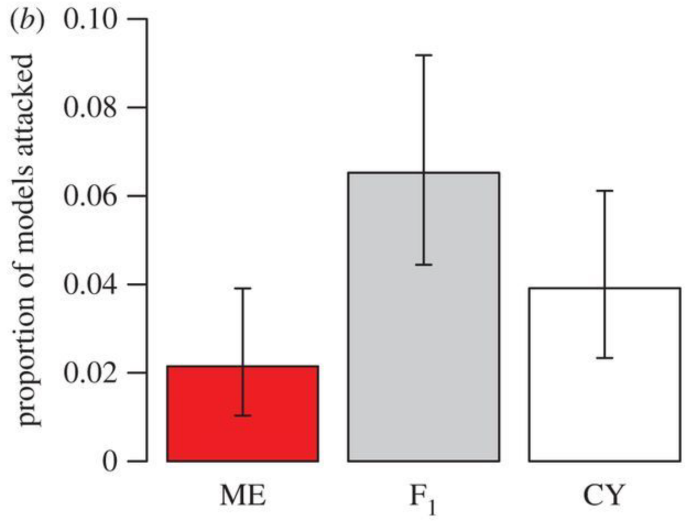
Hybrids are rare: 1 in 1000.

Nonetheless, ~40% of the genome is admixed

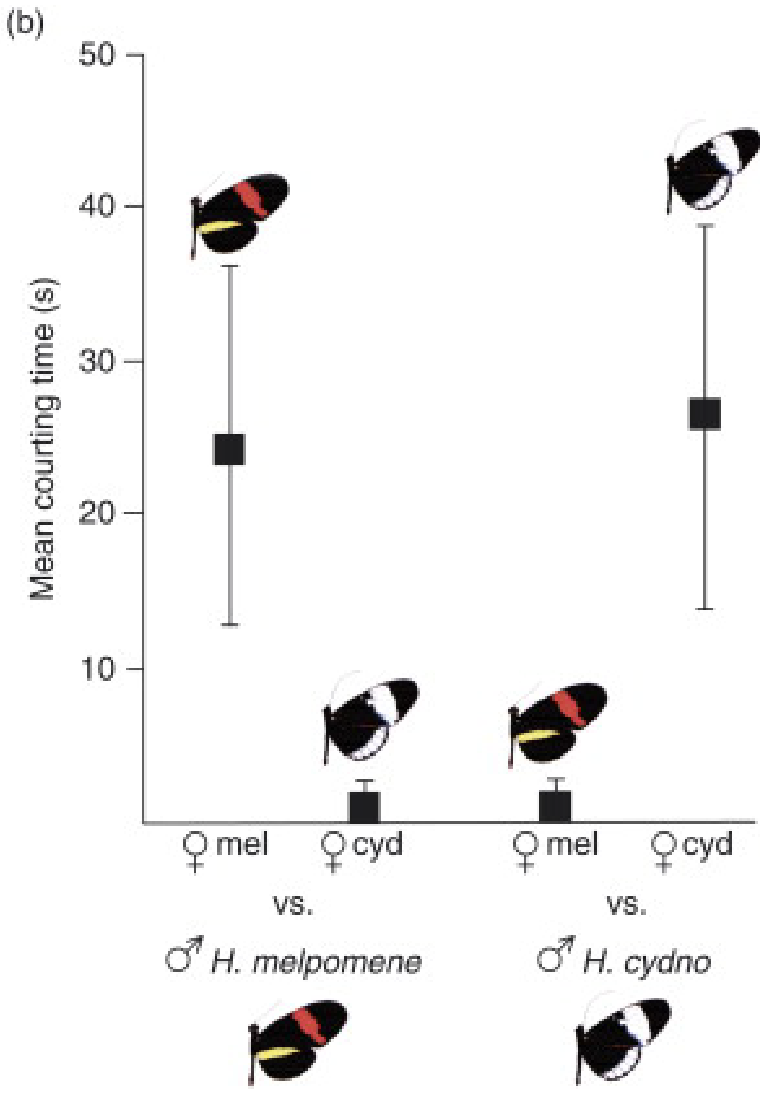
ME
(H. melpomene)

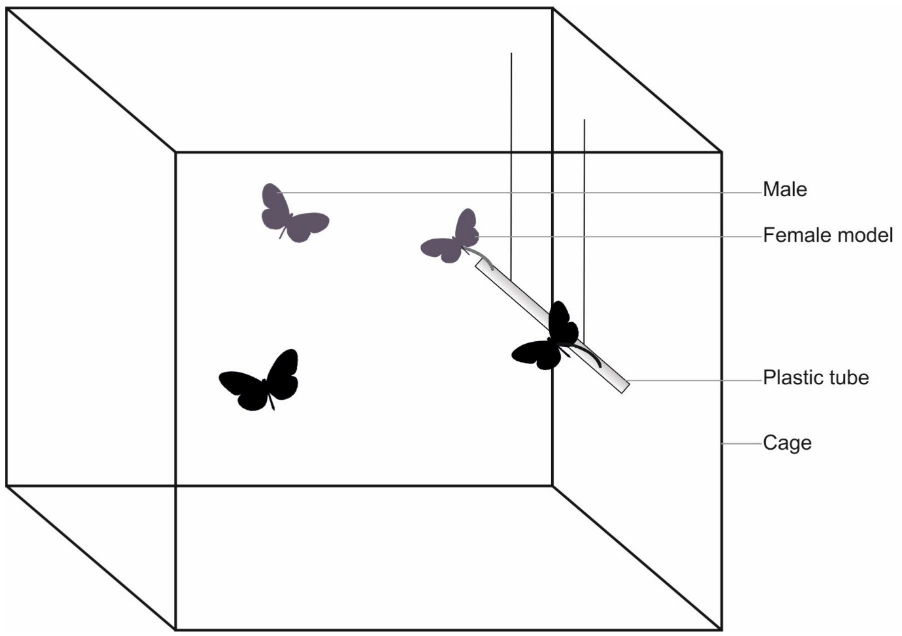
F1
hybrid

CY
(H. cydno)

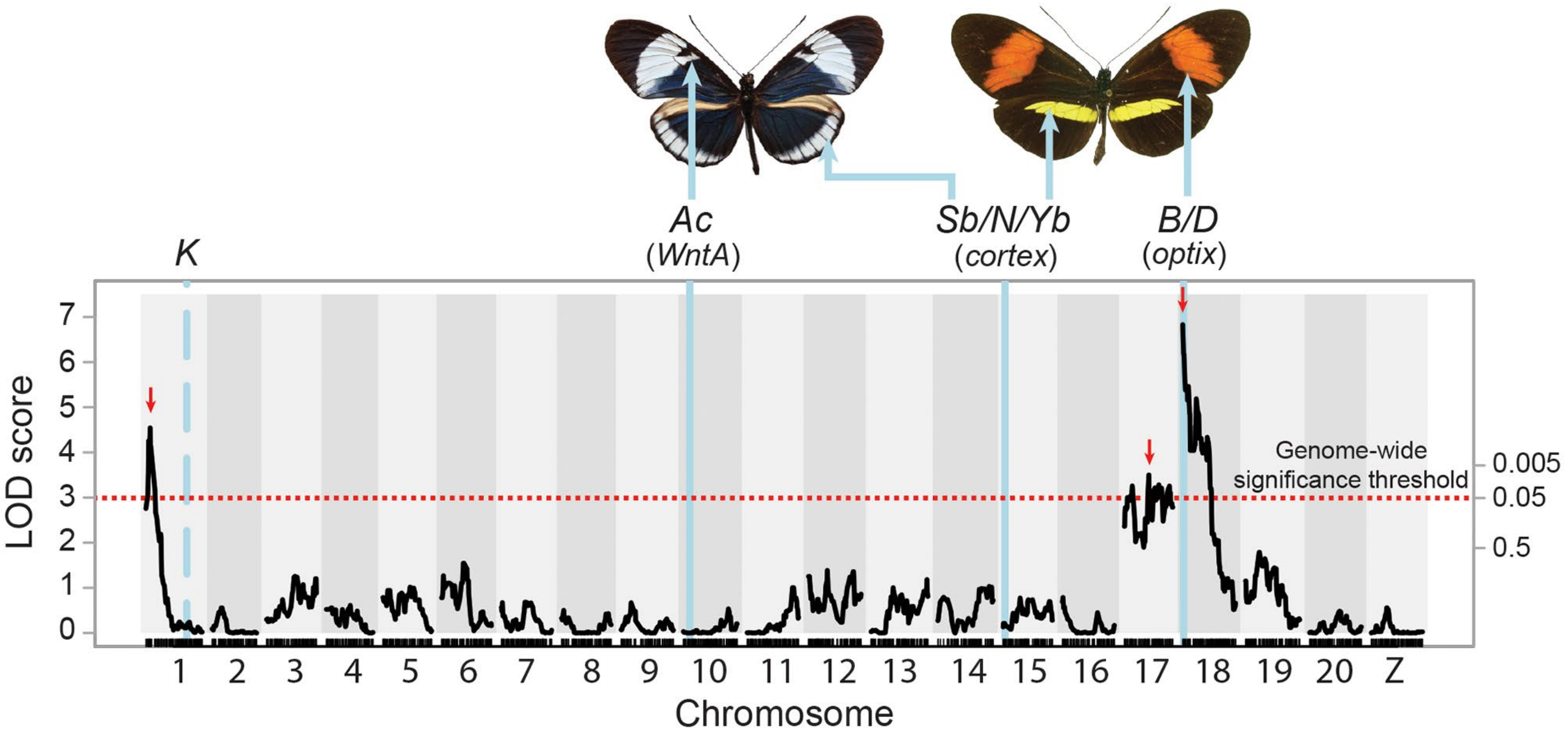



Merrill et al. 2012




Jiggins et al. 2012




PLOS | BIOLOGY

RESEARCH ARTICLE

# Genetic dissection of assortative mating behavior

Richard M. Merrill[1,2,3]*, Pasi Rastas[2], Simon H. Martin[2], Maria C. Melo[3,4], Sarah Barker[2], John Davey[2,5], W. Owen McMillan[3], Chris D. Jiggins[2]

# The 3 components of ecological speciation in *H. melpomene* and *H. cydno*

1) Divergent selection for mimicry by birds.
2) 2 forms of reproductive isolation:
    - Selection against non-mimetic intermediates in color patterns
    - Assortative mating based on color pattern
3) A genetic mechanism linking selection to RI
    - A single locus codes for color pattern and there is linked male preference for that color pattern

# And finally…

When is speciation not ecological?

Mutation-order speciation

Populations are subject to similar selection pressures, but (stochastically) evolve different solutions for adapting to them. These can then produce incompatibilities when the species come into contact.

Like non-adaptive radiations, it's hard to know how common this is.