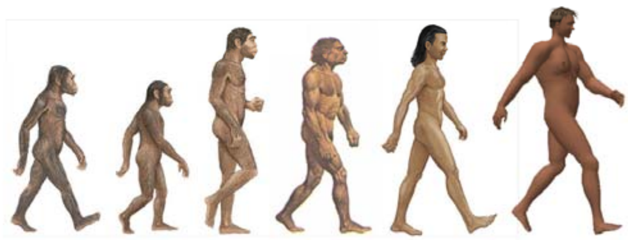
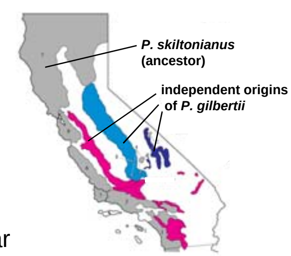
Speciation, continued

1. Geographical (**allopatric**) speciation, conclusion: the role of **ecology**
2. “**De-speciation**” (reverse speciation)
3. Primary and secondary **hybrid zones**
4. **Parapatric** and **sympatric** speciation
5. **Character displacement** and **reinforcement**



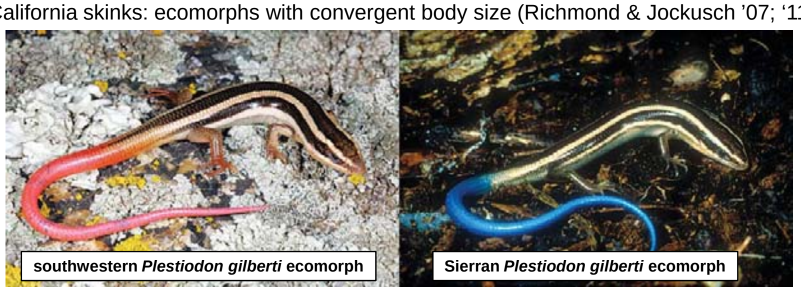
Parallel speciation supports an ecological driver

(criteria from Strecker et al. 2012, on Neotropical cave fish)



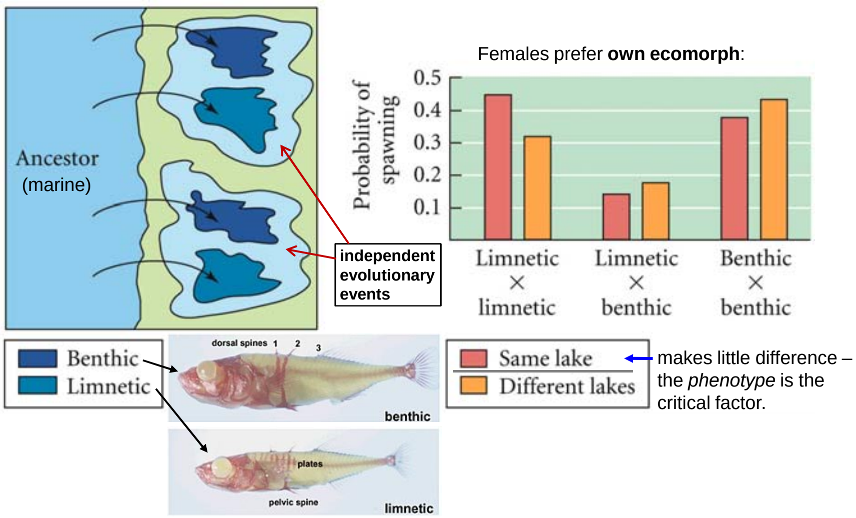
1. Separate populations in similar environments must be phylogenetically independent, such that shared traits responsible for reproductive isolation evolved separately.
2. Ancestral and descendant populations must be reproductively isolated.
3. Separate descendant populations inhabiting similar environments must not be reproductively isolated from one another.

California skinks: ecomorphs with convergent body size (Richmond & Jockusch ’07; ‘11)



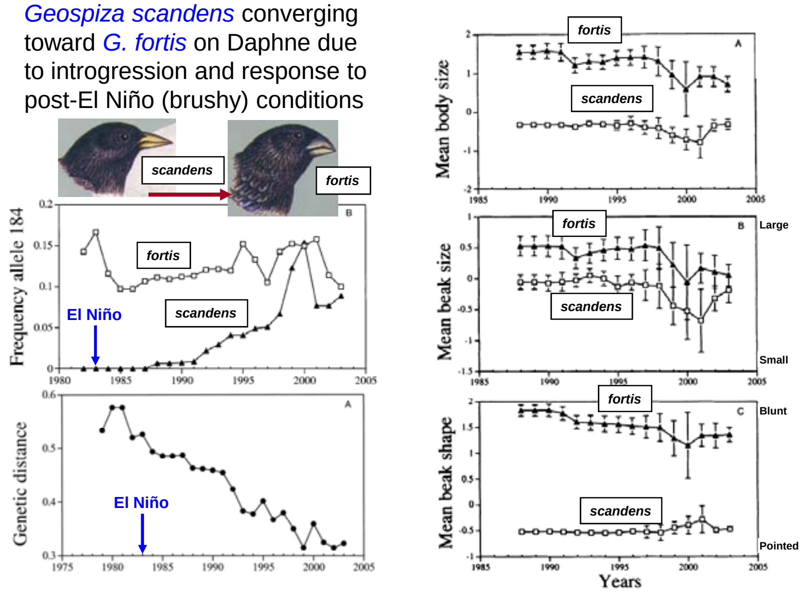
Parallel ecological speciation in the 3-spined stickleback, *Gasterosteus aculeatus* (after Schluter & Nagel 1995, Rundle *et al*. 2000)

Independent evolution of "**ecomorphs**"



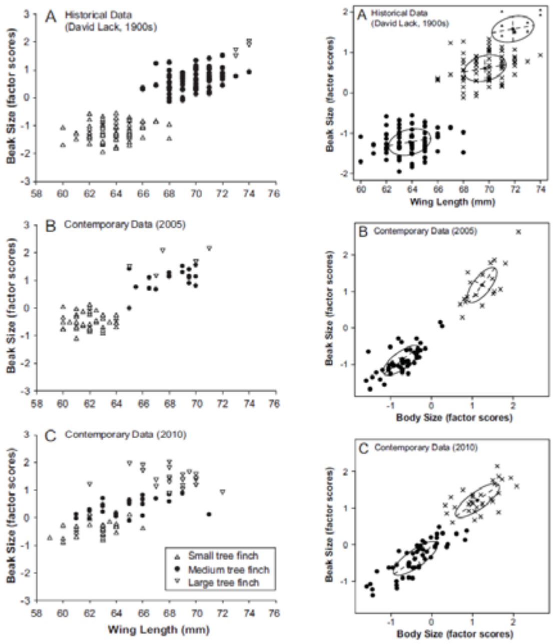
What Ecology gives, it can take away: **De-speciation** (Grant et al. 2004)

Geospiza scandens converging toward *G. fortis* on Daphne due to introgression and response to post-El Niño (brushy) conditions

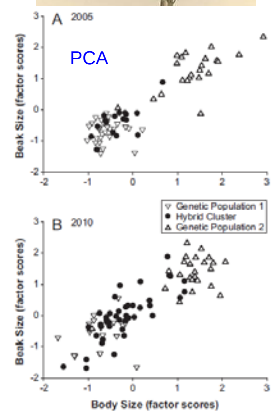


Bivariate plots

Cluster analysis



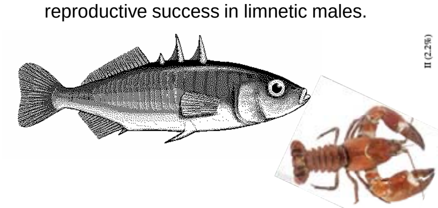
Three **tree finch species** in the Galápagos also show reverse speciation
(Kleindorfer et al. 2014)

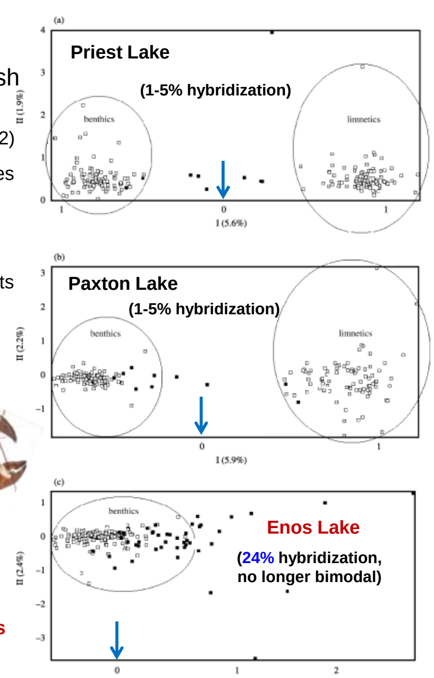


De-speciation in the benthic and limnetic species of stickleback in British Columbia

(Gow et al. '06; Taylor et al. '06; Velema et al. '12)

- Based on multilocus genotypes; filled squares are **hybrid** individuals.
- **Enos Lake** shows biased introgression of benthic ⟶ limnetic.
- **Reason**: An **invasive crayfish** which disrupts reproductive success in limnetic males.





Another example: Seehausen et al. 1997 on haplochromine cichlids in Lake Victoria and ***eutrophication***, causing misperception of color markings.

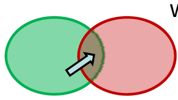
One possible spin-off: the **"Ephemeral Species Model"** (Rosenblum et al. 2012)

Speciation, continued: **The importance of hybridization**

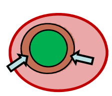
1. Hybridization has a general *negative* effect on speciation, by fusing two incipient species into a single species (**Mayr 1963** and other publications).
2. Hybridization completes speciation between incipient species, when *reinforcement* takes place in persistent hybrid zones (**Dobzhansky 1937**).
3. Also through reinforcement, hybridization permits non-allopatric (parapatric & sympatric) speciation.
4. Hybridization creates new "hybrid species" via introgression and recombination, at least in some plants (**Rieseberg 1997**) and a few animals.
5. If it involves unreduced gametes or is followed by chromosome doubling, hybridization can create new species nearly instantaneously.

Hybrid zones: Engines of speciation

"An area of contact between two noticeably different populations, in which hybridization takes place."

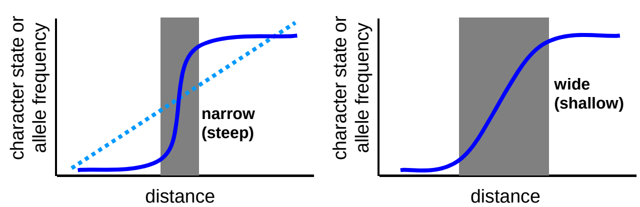


- may occur when previously allopatric populations meet → "***secondary* contact zone**" (allopatric speciation)



- or may occur within one contiguous species where two different forms of the species meet → "***primary* contact zone**" (parapatric/sympatric speciation)

Typically, a hybrid zone is a "**stepped cline**" across a discontinuity:



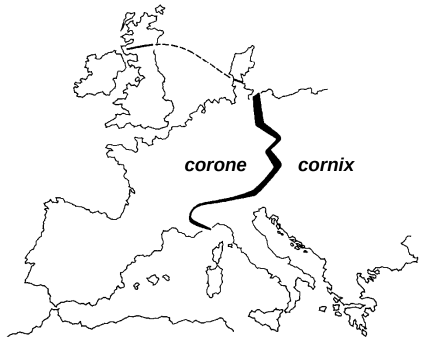
But may also take the form of a "**mosaic hybrid zone.**"

A typical, persistent, *clinal* hybrid zone:

Carrion vs hooded crow in Europe (after Mayr 1963)

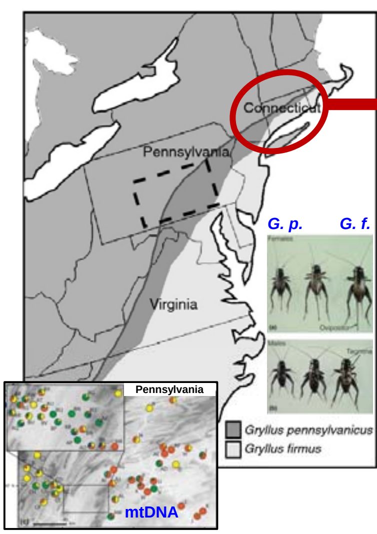
***Corvus corone* (carrion crow)**

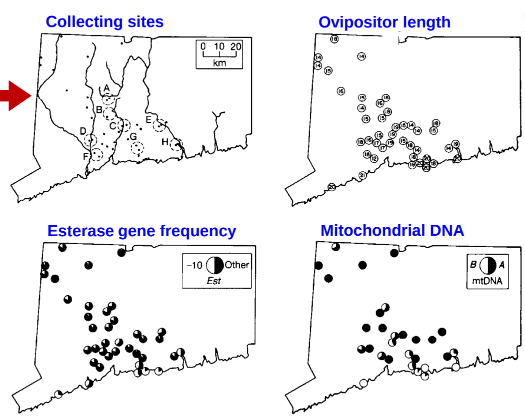
***Corvus cornix* (hooded crow)**



(Latest word: Poelstra et al. 2013 on hybrid zone genomics)

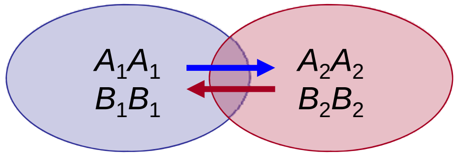
A **mosaic hybrid zone** in the crickets *Gryllus firmus* & *G. pennsylvanicus*
(after Harrison and Rand 1989; Larson…Harrison 2013)





Parental forms will be patchily distributed across heterogeneous habitat.

Genetic dynamics in a **hybrid "tension" zone**

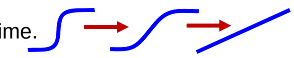


Assumptions:

I. $\boldsymbol{A_1A_2}$ has ***reduced*** fitness regardless of environment (say, because of B-D-M epistasis) – "selection against hybrids"

- Dispersal means allele A_1 will enter population 2 and A_2 will enter population 1.
- But neither A_1 nor A_2 will increase in frequency in the "wrong" population because of the heterozygote's disadvantage.
- It's a "standoff:" neither population's allele can invade the other population (this is the reason it's called a ***tension zone***).

II. $\boldsymbol{B_1B_2}$ has the ***same*** fitness as either homozygote (alleles are neutral).

- If *linked* with *A*, *B* alleles will share their fate with *A* (hitchhiking).
- If *not* linked with *A*, B_1 and B_2 alleles will diffuse through the hybrid zone and spread into the "wrong" population.
- The clines for these alleles get shallower over time. 
- This is ***introgression***.

Widths of hybrid zones (tension zones) vary significantly,
determined by strength of *selection* vs. *gene flow* (dispersal)

Very narrow hybrid zone:

Gaillardia pulchella, Texas: **a few meters**

Blanket Flower
(two chromosome races)

strong selection and/or
low dispersal (gene flow)

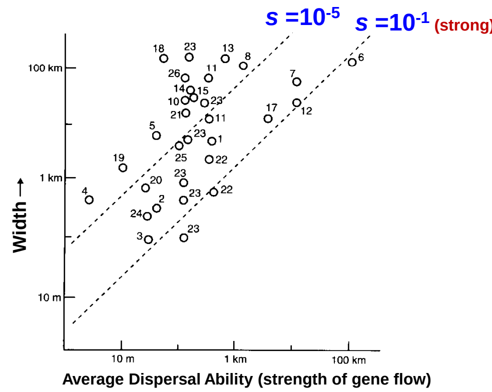
Broader hybrid zone:

Pinus muricata, California: **a few kilometers**

Bishop Pine
(southern & northern color morphs)

The **width** of a hybrid zone is a function of the ***selection intensity on*** and the ***dispersal ability of*** taxa – i.e., **balance** between **selection** & **migration**.

(data from 26 genera; Barton & Hewitt 1985)



(*s* = selection against heterozygotes)

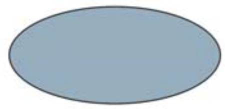
Hybrid zones vis-à-vis types of speciation

1. **Geographical (allopatric/peripatric) speciation**
   - geographical isolation (barrier to gene flow)
     - may involve dispersal or vicariance
   - genetic divergence due to chance or selection
     - postzygotic genetic incompatibilities
     - reinforcement of prezygotic isolation
2. **Non-allopatric speciation**
   - **Parapatric/sympatric speciation**
     - disruptive selection (ecological)
     - development of assortative mating via:
       - reinforcement of prezygotic isolation
       - sexual selection
   - **Polyploidy** and **interspecific hybridization**
     - autopolyploidy
     - allopolyploidy
   - other sympatric modes, e.g., **recombinational speciation; homoploid hybrid speciation**

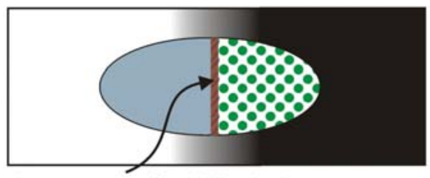
interactions in hybrid zone

Parapatric Speciation (nearly the same as sympatric speciation)

(1) Ancestral population (homogeneous)



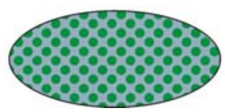
(2) Strong environmental gradiant, differentiation occurs



(*divergent selection along an environmental gradient*)

(narrow zone of hybridization) – a zone of "**primary contact**" (primary hybrid zone)

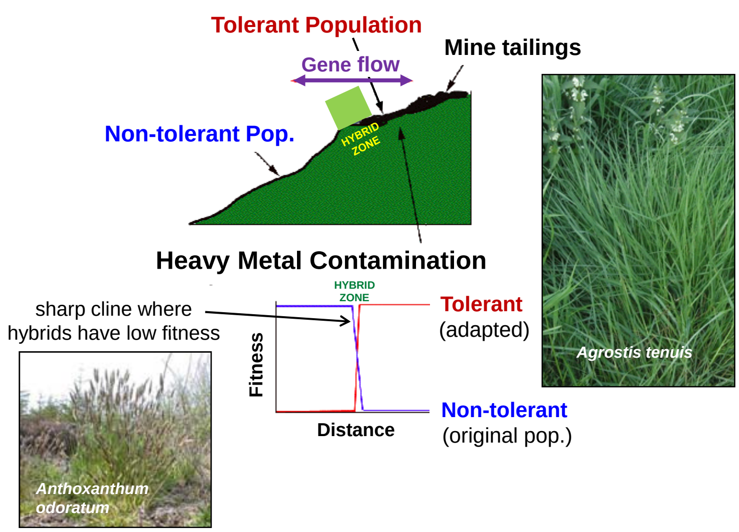
(3) Two sympatric, non-interbreeding species are established



Stage 3 is a problem! – how is gene flow cut off?

Heavy metal tolerance and hybrid zones in *Agrostis tenuis* and *Anthoxanthum odoratum*

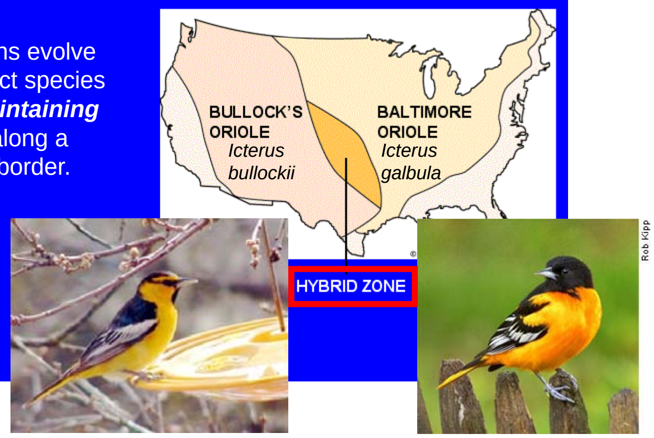
(*divergent selection along an environmental gradient*)



Parapatric speciation, or just secondary contact?

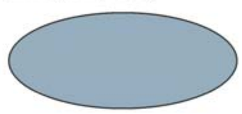
Evidence from the field is often ambiguous.

Adjacent populations evolve into distinct species ***while maintaining contact*** along a common border.

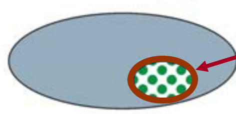


Sympatric Speciation

(1) Ancestral population (homogeneous)

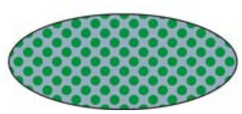


(2) New population appears within ancestral population



(think of this population as **surrounded by a narrow zone of "primary contact" (brown) --- a primary hybrid zone**)

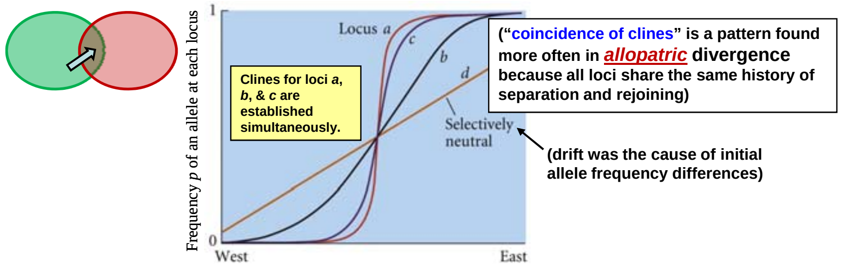
(3) Two sympatric, non-interbreeding species are established



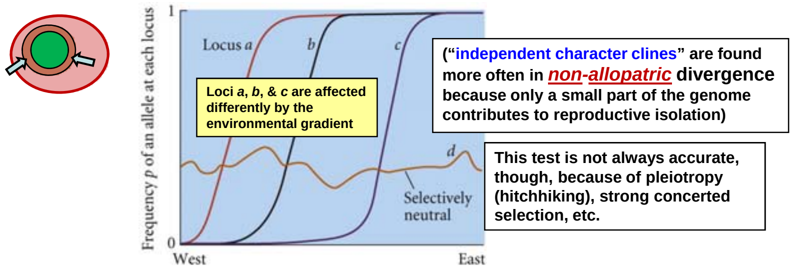
*Again, **stage 3** is a problem!* The hybrid zone provides the answer.

Distinction between **secondary** vs. **primary** hybrid zones

Secondary hybrid zone: __between__ populations or species; due to secondary contact

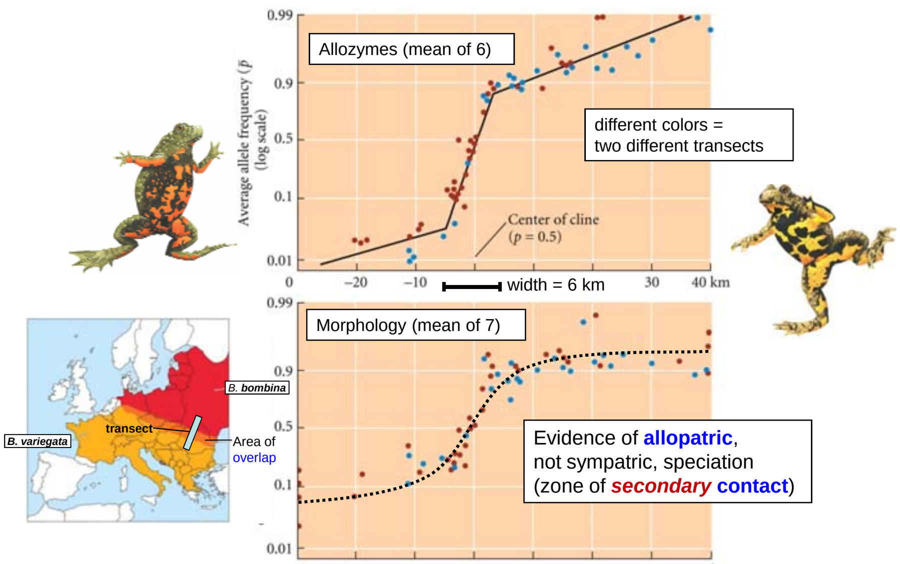


Primary hybrid zone: __within__ a single population; due to an environmental discontinuity

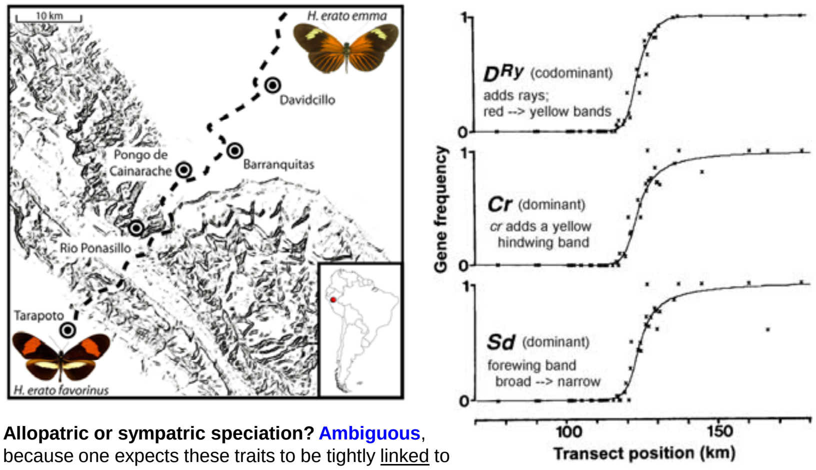


Coincidence of character trait variation across a stepped cline:

Hybrid "tension" zone in Poland between fire- and yellow-bellied toads, *Bombina bombina* & *B. variegata* (after Szymura 1993)



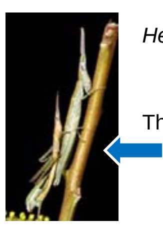
Clines in hybrid zone of *Heliconius erato favorinus* and *H. erato emma* in Peru (Mallet et al. 1998, Counterman et al. 2010)



Allopatric or sympatric speciation? Ambiguous, because one expects these traits to be tightly linked to achieve convincing mimicry (very strong **ecological selection** exists). More about *Heliconius* later!

The fate and function of hybrid zones

1. If the lower fitness of hybrids is due to *epistasis* or a *steep, fixed ecological gradient*, the hybrid zone can persist indefinitely – the zone is **stable**, e.g.:



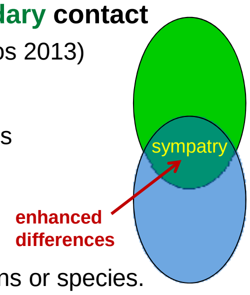
Heliconius hybrid zones in NE South America have persisted for 200 years (Turner, Jiggins, Mallet, McMillan, Brower – many papers).

Three chromosomal forms of the grasshopper *Warramaba* meet in a hybrid zone on Kangaroo Island, S. Australia, which is thought to have been stable for 8,000-10,000 years! (Lewontin 1960, White & Contreras 1979).

2. If alleles *improving fitness of hybrids* appear and increase, the two entities may fuse into one.
3. Natural selection may favor alleles that *enhance* ***(reinforce)*** *prezygotic reproductive isolation* between the two forms.
4. Some hybrids may become reproductively isolated from both parents and become a third species (*recombinational* speciation).

Reinforcement and other interactions occur between or within species in zones of primary or secondary contact

(Pfennig & Pfennig 2012; but see Stuart & Losos 2013)



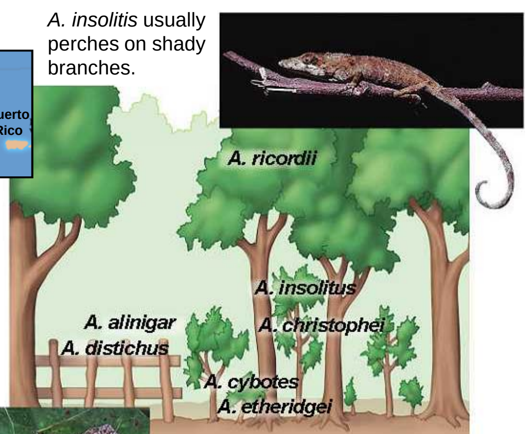
1. ***Ecological Character Displacement***
   - due to ecological interactions between species
2. ***Ecological Character Release*** (ditto above)
   - flip side of character displacement
3. ***Reproductive Character Displacement***
   - due to sexual interactions **between** populations or species.
4. ***Reinforcement*** (Dobzhansky 1937)
   - restricted to sexual interactions between populations **within** one species: "incipient species"

All are a consequence of ***resource competition*** of one sort or another occurring in the hybrid zone.

Same pattern is predicted for all: ***Higher levels of character differences in areas of sympatry than in areas of allopatry.***

Character displacement (resource partitioning) in *Anolis* lizards of Hispaniola (Losos 1992)

A. insolitis usually perches on shady branches.



A. distinchus perches on fence posts and other sunny surfaces.

Initial invasion: occupation of major habitat types.
Subsequent evolution: fine-tuning of ecological requirements.