

1. **Ecological Character Displacement**

- due to ecological interactions between species

2. **Ecological Character Release** (ditto above)

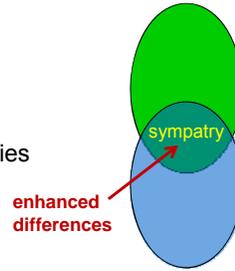
- flip side of character displacement

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"

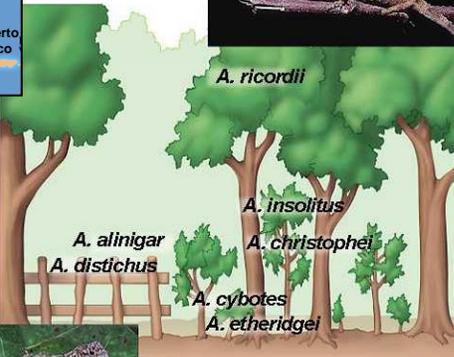


(Pfennig & Pfennig 2012;
but see Stuart & Losos 2013)

Ecological character displacement (resource partitioning) in
Anolis lizards of Hispaniola (Losos 1992)



A. insolitus usually perches on shady branches.

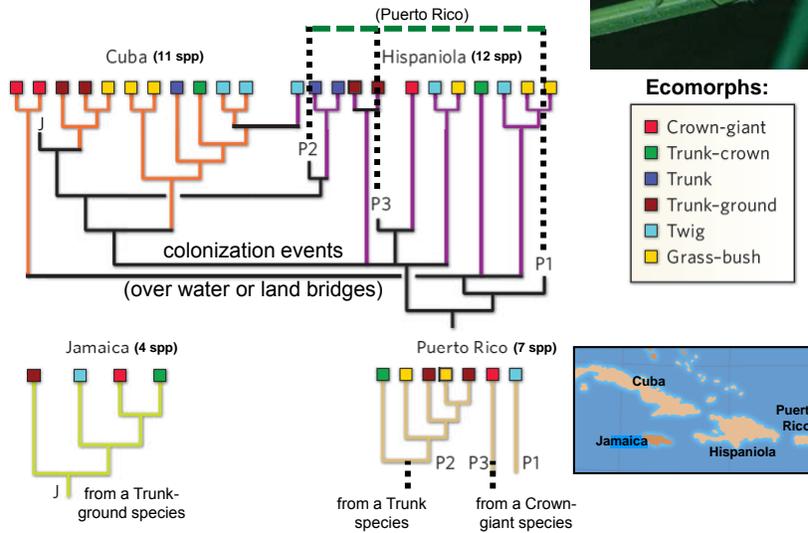


A. distinchus perches on fence posts and other sunny surfaces.



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

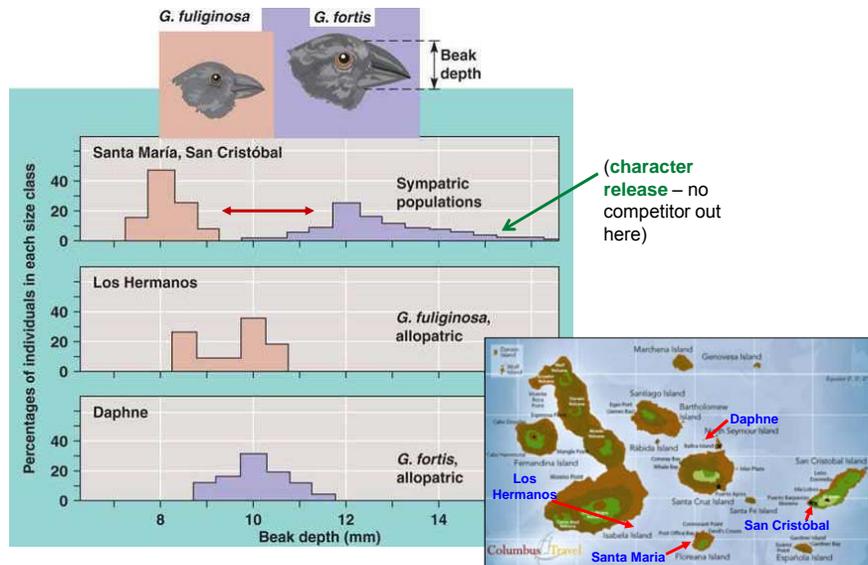
Character displacement (resource partitioning) in 34 Caribbean *Anolis* lizards
(E. E. Williams, many papers; Losos & Ricklefs 2009)



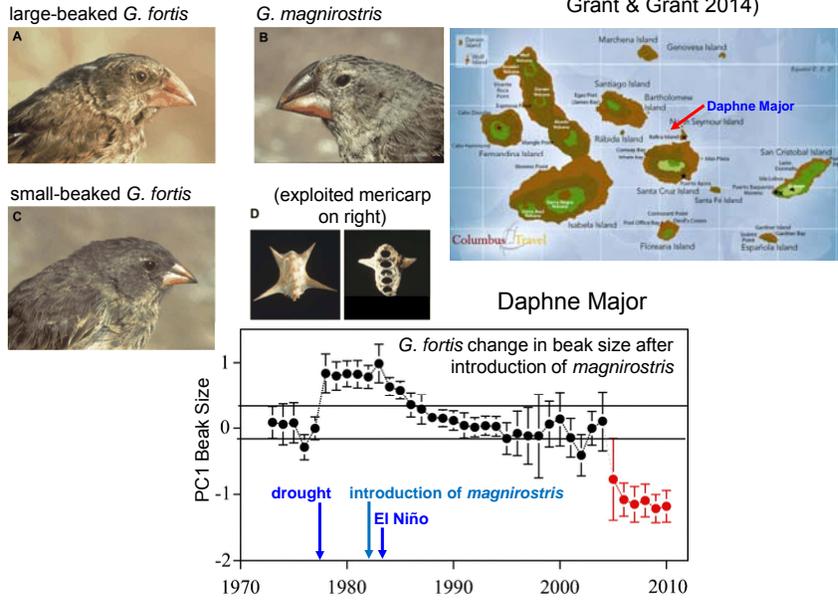
Ecomorphs:

- Crown-giant
- Trunk-crown
- Trunk
- Trunk-ground
- Twig
- Grass-bush

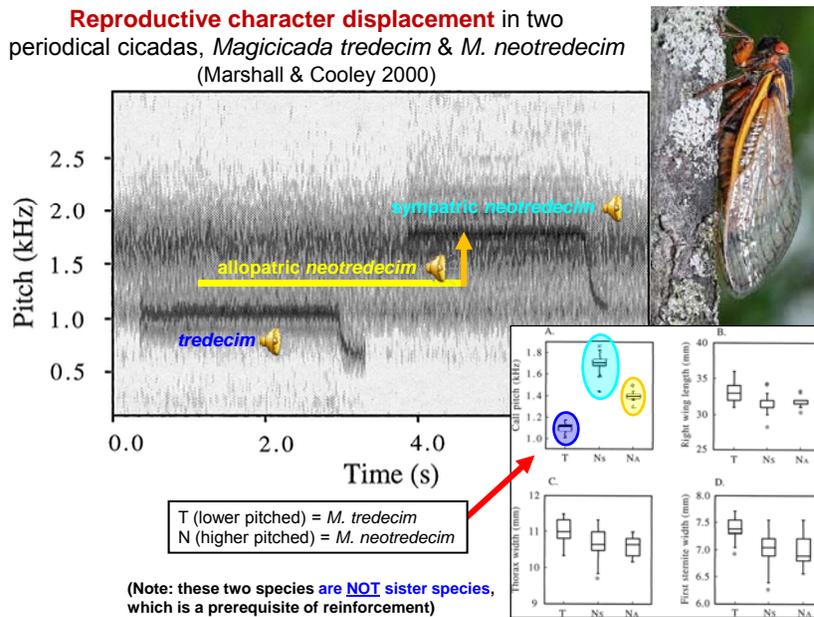
Character displacement in Galapagos Finches (from Lack 1940)



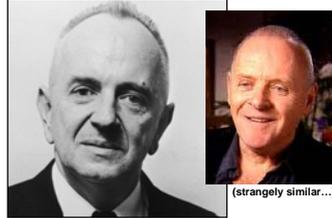
Character displacement in Galapagos Finches, II (Grant & Grant 2006; Grant & Grant 2014)



Reproductive character displacement in two periodical cicadas, *Magicicada tredecim* & *M. neotredicim* (Marshall & Cooley 2000)



Reinforcement is a special form of reproductive character displacement, but it can only take place between populations *that are not yet reproductively isolated from each other* (Butlin 1987).



- First proposed by Wallace; modern idea is from Dobzhansky (1937).
 - Dobzhansky considered it of *great importance* in speciation.
 - Mayr (1963): Minor compared to “epistatic incompatibilities.”
 - 75 years of acceptance and rejection...
 - ...and it remains controversial.
-
- Very difficult to distinguish from other types of character displacement between ‘good’ species, because *both generate the same patterns*.
 - It **completes** speciation – **stage 3**. It’s optional in allopatric speciation, but mandatory in most ecological scenarios of non-allopatric speciation.

The specific conditions favoring reinforcement

1. Two populations exist, each associated with a different environment.
2. A hybrid (tension) zone exists between them (primary or secondary).
3. In the zone, hybrids have **low** fitness (lower than parents), but *not zero* fitness – hybrids experience negative selection.
4. One locus specifies environmental (ecological) **adaptation** and a second one appears that specifies **assortative mating** (mate choice)
 - These two loci should be strongly **linked** – or one locus specifies BOTH adaptation and assortative mating (Gavrilets’ “**magic trait**”)
 - If linkage is weaker, then **recombination** must be low – i.e., assortative mating and/or habitat choice must be high.
 - The process is enhanced by *two co-evolving assortative mating loci*: a mating trait, and a preference for that trait (a price paid for two sexes)
5. Natural selection then favors the evolution of **pre-mating barriers (assortative mating)**, which cut off gene flow by stopping the formation of hybrids.
6. Speciation is completed! (**Stage 3 is done**)

(genetics must be simple)

Important aside: Reinforcement can only strengthen *prezygotic* reproductive isolation: alleles that confer lethality (intrinsic **postzygotic** isolation) can never be favored.

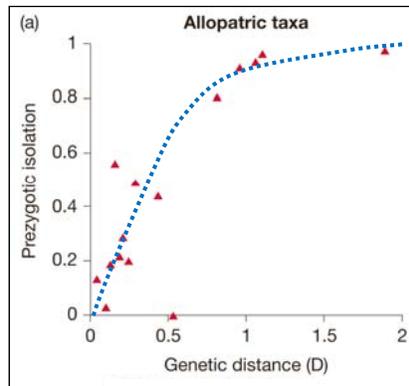
Coyne & Orr's (1997) survey of over **150 *Drosophila* species-pairs**:
Looking for a **pattern consistent with reinforcement**



- Are the species in a pair allopatric or sympatric?
- What is the genetic distance between the species of each pair? (based on allozymes -- a surrogate for *elapsed time*)
- What is the level of postzygotic and prezygotic isolation between the species of each pair?



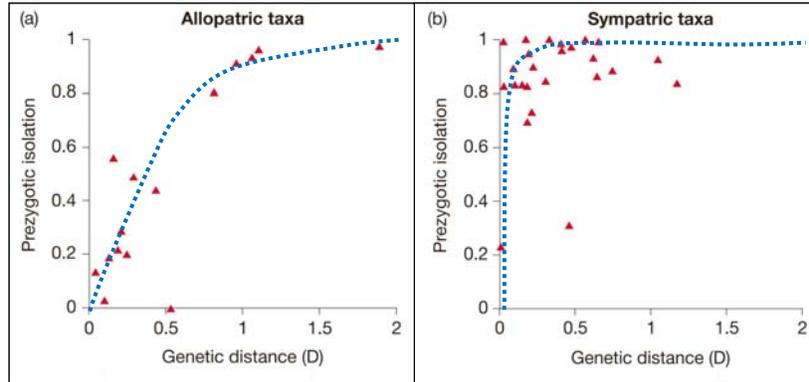
Remember that a prerequisite for reinforcement is the formation of hybrids with some viability, otherwise it's just reproductive character displacement.
(Butlin 1987)



Prezygotic isolation increases **steadily** with genetic distance.

Alleles for prezygotic isolation diverge over time, just like the rest of the genome.

(Coyne & Orr '97)



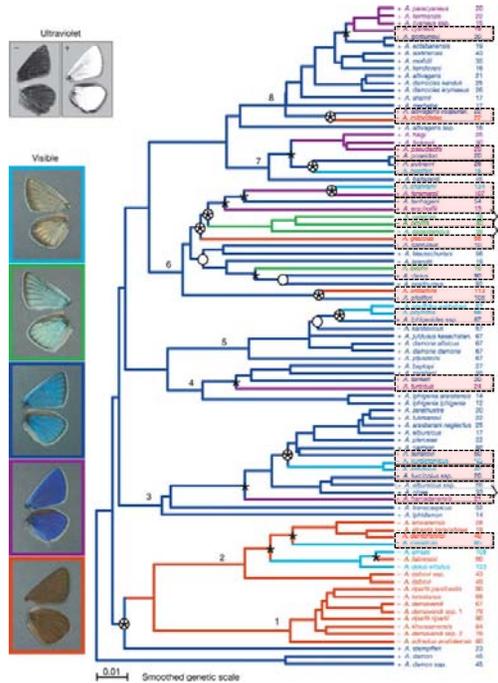
Full prezygotic isolation evolves in either allopatry or sympatry, but **much faster in sympatry**.

Nothing else is needed to complete the speciation process; reinforcement is supported.

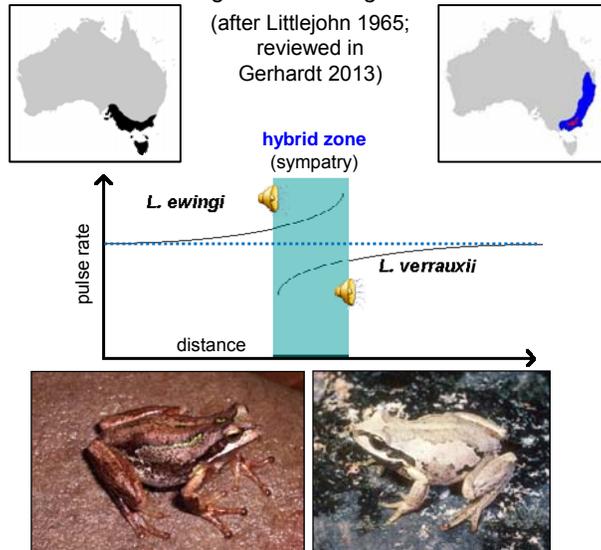
(Coyne & Orr '97)

Phylogenetic patterns consistent with reinforcement of color in lycaenid *Agrodiaetus* butterflies. (Lukhtanov et al. 2005)

- Boxes on right mark relatively **young sympatric** pairs of taxa with markedly different visible colors.
- +/- codes UV reflectance or lack of same.
- (haploid chromosome numbers in column on right)

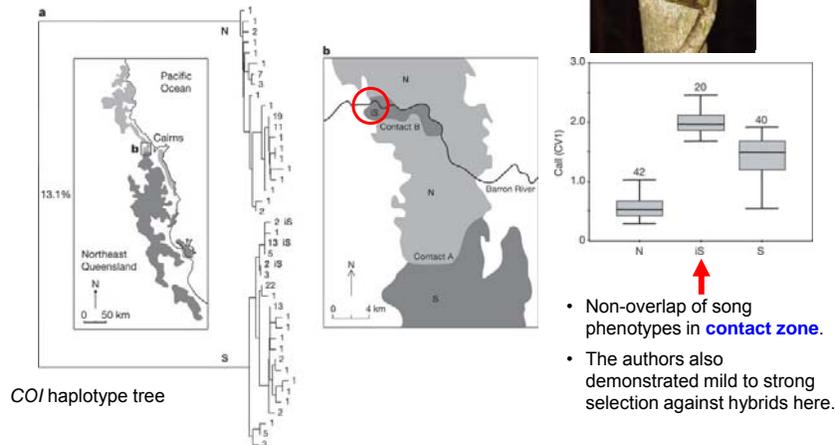


Another classic example: Reinforcement of **song** differences in the Australian tree-frogs *Litoria ewingi* and *Litoria verreauxi*

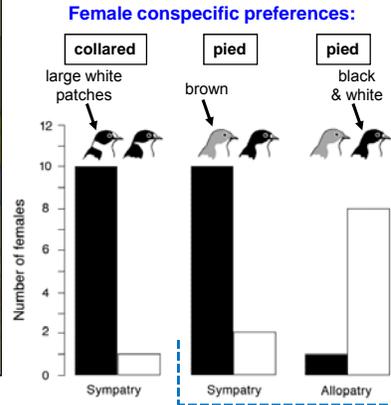
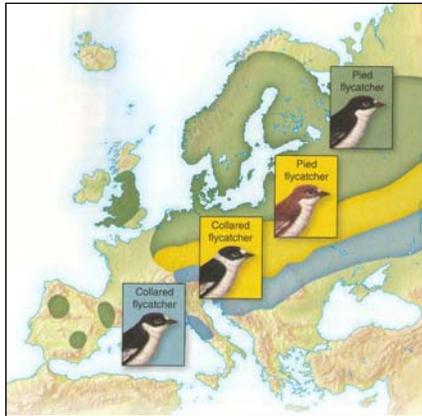


Other convincing examples of this rather elusive process follow:

Evidence for **reinforcement of songs** in two “populations” of the green-eyed tree frog, *Litoria genimaculata*, in northeastern Australia (Hoskin et al. 2005)



Evidence for **reinforcement** of **color** in the flycatchers *Ficedula hypoleuca* (pied) & *F. albicollis* (collared) in Europe (Saetre et al. 1997; Saetre & Saether 2011)

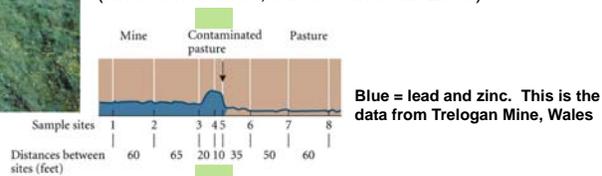


The authors claim to show that the resulting character displacement reduces the frequency of hybridization in areas of secondary contact.

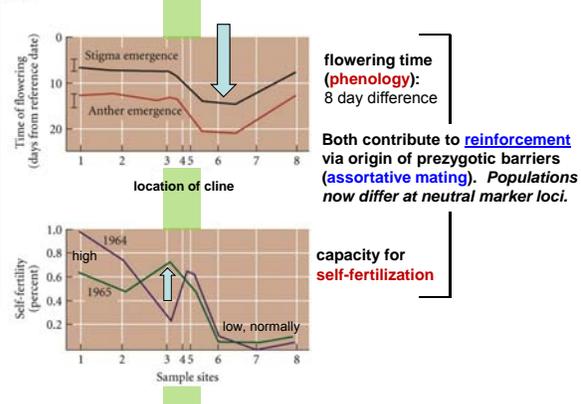


Reinforcement of phenological and mating system differences in 150 years

(Antonovics 1968, Silvertown et al. 2005)



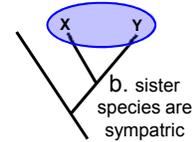
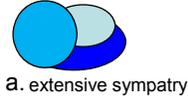
Anthoxanthum odoratum (European bunchgrass)



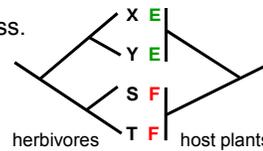
Evidence for parapatric / sympatric speciation:
 i.e., “non-allopatric speciation” or “speciation with gene flow”
 Coyne & Orr 2004, Coyne 2011; Bolnick & Fitzpatrick 2007

I. Pattern consistent with the process.

- Simplest one: *closely-related members of a monophyletic clade of recent origin are extensively sympatric.*
- Closely related sister species (X & Y) are mutually sympatric.
- Sister-species pairs are associated with single hosts (or sister-species host pairs).
- Other phylogenetic, ecological, behavioral, or genetic patterns.



c. sister species share host

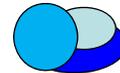


II. Mechanism / theory to explain the process.

III. Examples from nature (the “isolated island method” is a good approach, i.e., Coyne’s “speciation in a small place”

I. Pattern-based evidence:

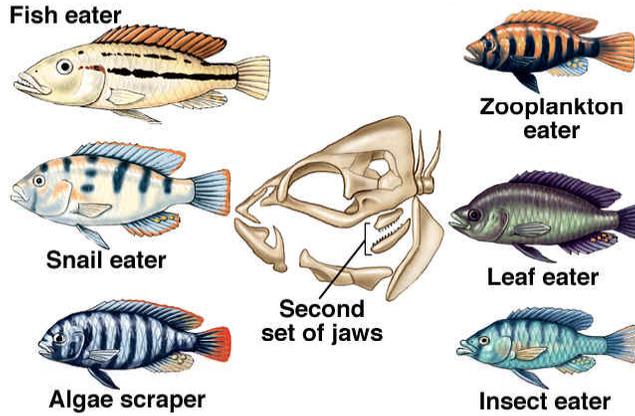
Lake Victoria: 500 species of Cichlidae
 from one founder, 14,600 yrs ago.
 (Meyer 1990, Johnson *et al.* 1996)



Mating decisions are based largely on **ecology** and on **color** hue and pattern in sister species.

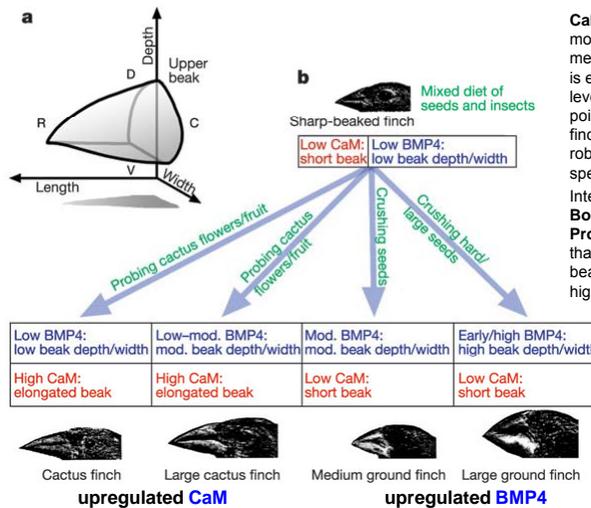


Details: **Haplochromine Cichlidae** show nearly every type of feeding adaptation one could imagine...so **ecology** – and a second set of jaws – have obviously played a role in diversification.



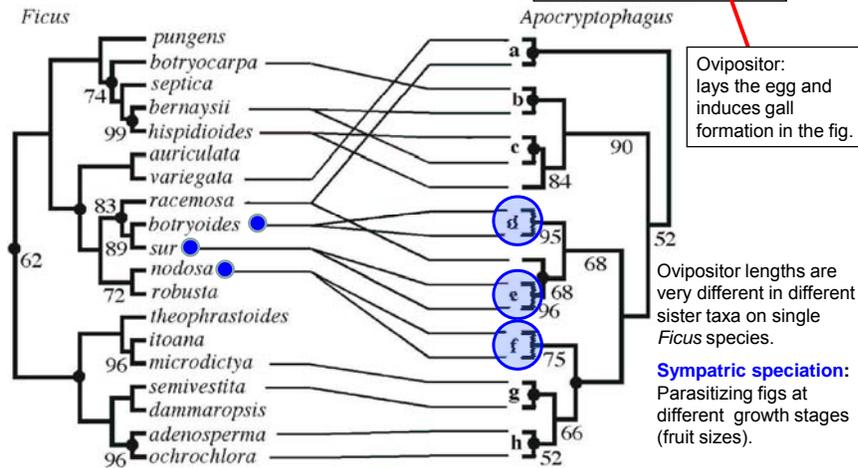
Amazingly, the same signaling molecule (**BMP4***) is involved in the development of large and deep beaks in Darwin's Finches (Grant & Grant 2006) [* = bone morphogenic protein]]

Regulatory agents controlling beak proportions in Darwin's Finches (Abzhanov et al. 2006)



Calmodulin (CaM), a molecule involved in mediating Ca^{++} signaling, is expressed at higher levels in the long and pointed beaks of cactus finches than in more robust beak types of other species. Interacts as shown with **Bone Morphogenetic Protein 4 (BMP4)** such that large blunt (deep) beaks are produced by high BMP4 and low CaM.

Phylogenetic pattern consistent with sympatric speciation in **parasitic fig wasps**, based on COI phylogeny (Weiblen & Bush 2002)



Note: The **mutualistic** fig wasp species largely show pairwise co-evolution with fig species

II. **Mechanism/Theory** supporting sympatric speciation

A. Disruptive Natural Selection

1. **Discrete niche/habitat models** (“multiple niche polymorphism”)
 - a. **Niche adaptation** and **assortative mating** (Maynard Smith 1966, Felsenstein 1981) – e.g., possibly lacewings (*Chrysoperla*)
 - b. **Niche adaptation** and **niche preference** (Diehl & Bush 1989, Fry 2003, Kawecki 1996, 1997) – e.g., *Rhagoletis*
 - c. **Niche preference** and **assortative mating** (Rice 1984, 1987) – e.g., *Chrysoperla*
 - d. **Niche adaptation**, **niche preference**, and **assortative mating** (Johnson et al. 1996) – theory only
2. **Continuous-resource models** (“adaptive” or “ecological” speciation)
 - a. **Unimodal** resource distribution (Seger 1985, Dieckmann & Doebli 1999) – work best with “**magic traits**” (combining competition with assortative mating)
 - b. **Bimodal** resource distribution (Kondrashov 1999)

B. Disruptive Sexual Selection (more later)

1. **Mate preference** functions (Turner & Barrows 1995, Higashi et al. 1999)
2. **Sexual conflict** (Gavrilets & Waxman 2002)
3. **Sexual selection** plus **niche differences** (Payne & Krakauer 1997)
4. Disruptive **natural selection** favors the evolution of sexual **preferences** for ornaments that signal local adaptation (van Doorn et al. 1998, 2009)
5. **Mutual mate choice** (Almeida & Abreu 2003, Puebla et al. 2012)

Disruptive Natural Selection:
Maynard Smith (1966) – a population genetic model of (A-1a) multiple niche polymorphism



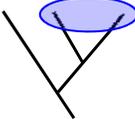
John Maynard Smith

1. One 'host' or 'habitat' locus, **A (niche adaptation)**
 - 2 alternate alleles, A_1 and A_2 , for different hosts or habitats;
 - Heterozygote, A_1A_2 , is not well adapted to either;
 - Each homozygote (A_1A_1 or A_2A_2) would have a higher fitness if it mated assortatively.
2. A second 'assortative mating' locus, **B (assortative mating)**
 - 2 alternative alleles, B_1 and B_2 , which are responsible for preventing mating between the different host genotypes...
 - e.g., B_1B_1 and B_1B_2 might prefer to mate among themselves, to the exclusion of B_2B_2 .

Caveats: (and note similarity to reinforcement)

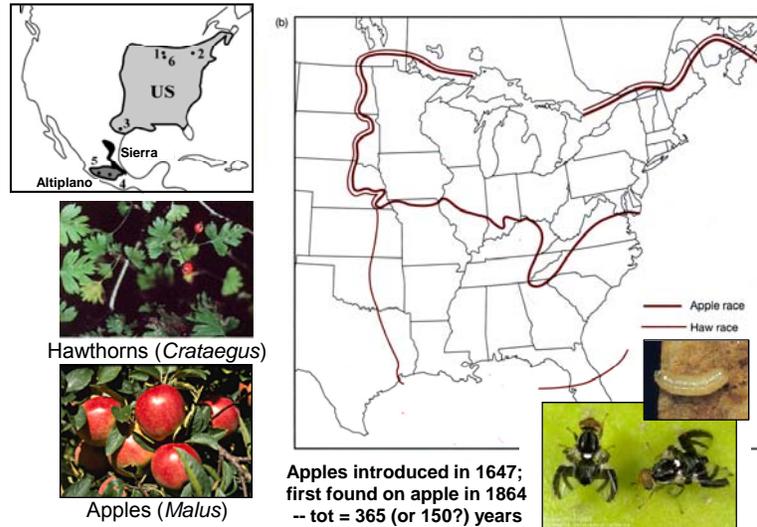
1. The 'host' and 'assortative mating' loci (**A & B**) must be strongly linked (or pleiotropic in some other way); i.e., "**magic traits**."
2. As few loci as possible must control niche choice and mate choice – preferably one each, as above.

In nature (not theory), what do we need to be convinced of sympatric speciation?

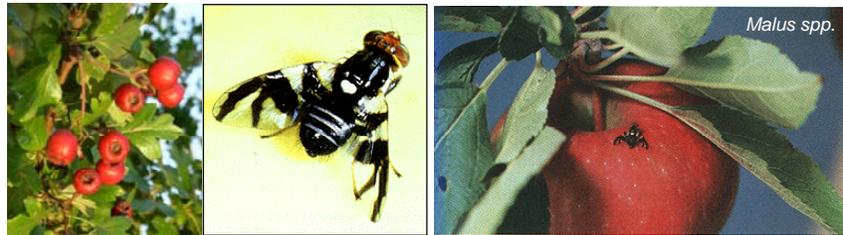
1. Species sympatry 
2. Sister relationships 
3. Reproductive isolation
4. that an earlier allopatric phase is highly unlikely

(Coyne & Orr 2004)

(A-1b) A well-studied case of putative sympatric speciation by disruptive selection:
 Differentiation of **host races** of *Rhagoletis pomonella* (Guy Bush, 1966 onward)



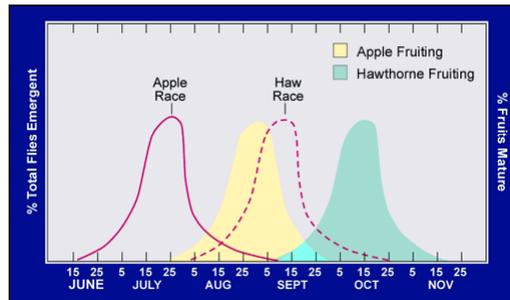
Rhagoletis pomonella 2 – **Change in life cycles** of the two host races due to niche preference & incidental assortative mating (allochronic isolation)



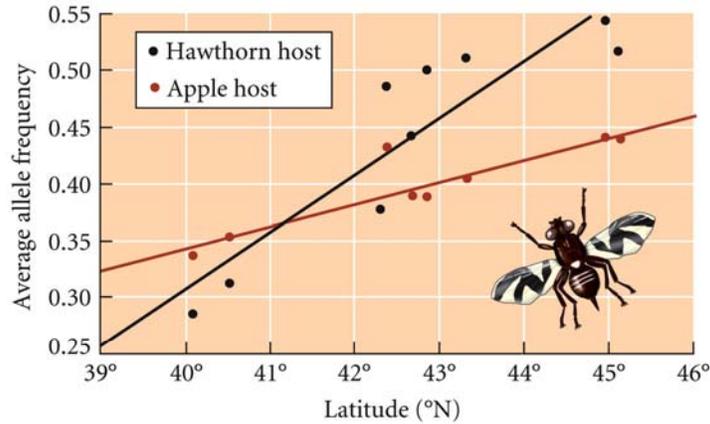
Days to maturation:

- Hawthorn: 55-60
- Apple: 40

Host fidelity has evolved – thereby *linking niche adaptation with assortative mating* and minimizing recombination -- (**magic trait**).



Rhagoletis pomonella 3 -- **Genetic differentiation** in the two host races at (possibly) neutral marker loci (after Feder et al. 1990)



(exchange of “neutral” alleles between races ≈ 2 percent)

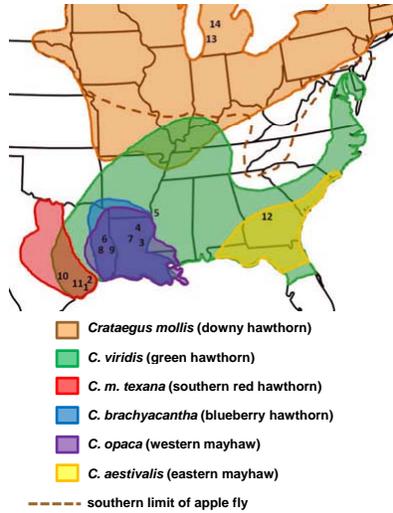
Rhagoletis pomonella 4 – A fly in the ointment: the populations in Mexico bearing **inversion polymorphisms** (Feder et al. 2003a, b; 2005; Rull et al. 2010)



“EVTM” region of Mexico:
 inversions on three chromosomes (of 6 total)
 host = *Crataegus mexicana* (tejocote)

- Alleles affecting diapause traits involved in host race formation reside within **large complexes of rearranged genes**.
- Episodes of gene flow from Mexico subsequently infused the North American population with **inversion polymorphism** affecting key diapause traits, forming adaptive clines.
- This diapause variation in the latitudinal clines appears to have aided North American flies in **adapting to a variety of plants with differing fruiting times**, helping to spawn several new taxa.
- Important **raw genetic material** facilitating the adaptive radiation of *R. pomonella* originated in a different time and place than the proximate ecological host shifts triggering sympatric divergence.

Rhagoletis pomonella 5 – Also: Standing variation for olfactory recognition **has to come from somewhere** (Powell et al. 2012)



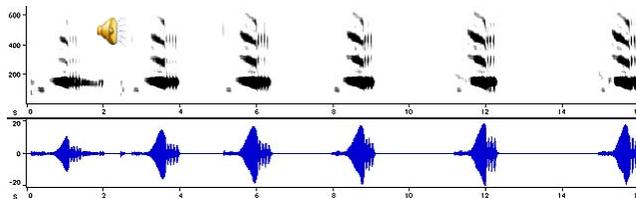
- *C. mollis* shares few volatiles with apples, so it's not clear how the apple maggot made the jump to apple when it's so different.
- The Mexican populations don't help, there's no evidence for introgression of apple preference from EVT.M.
- Southern species of *Crataegus* have the missing volatiles, so southern *R. pomonella* could have been preadapted for apple preferences via the southern hawthorns.
- And there are host races of *Rhagoletis pomonella* on those 5 additional hawthorn species.
- But southern hawthorn populations were not the antecedents of a preassembled apple race, based on those races not being attracted to the apple blend of volatiles.

(A-1b) Sympatric speciation by **host-race divergence** in the treehopper species complex, *Enchenopa binotata* (Tom Wood, Rex Cocroft, et al.)



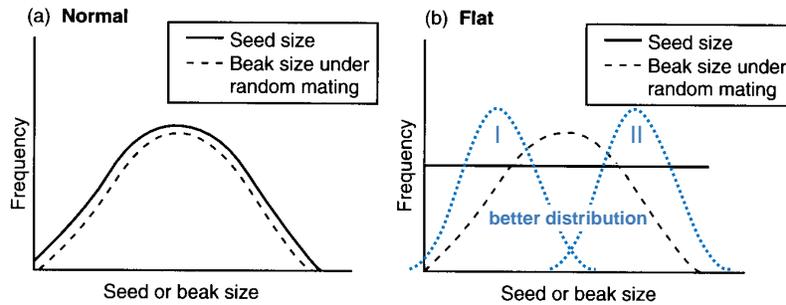
- on *Cercis canadensis* (redbud)
- on *Celastrus scandens* (native bittersweet)

- **Distinct phenologies** of the different hosts alter the timing of the life cycles through egg hydration, such that overlap of reproduction is greatly reduced, as in *Rhagoletis pomonella*.
- Simultaneous changes in **song phenotypes** may reinforce premating isolation.



Disruptive Natural Selection

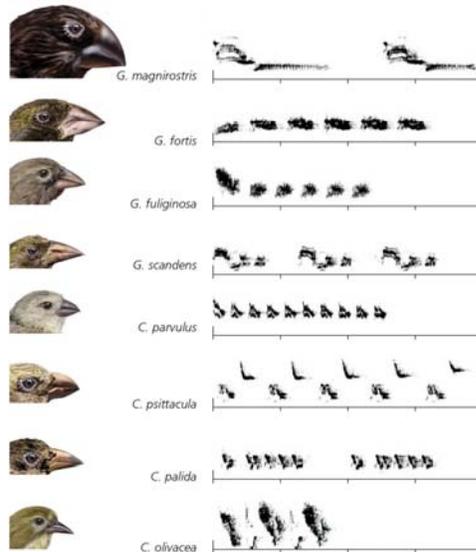
(A-2a) Seger's **unimodal continuous-resource model** (1985), developed from Bengtsson's original proposal (1979)



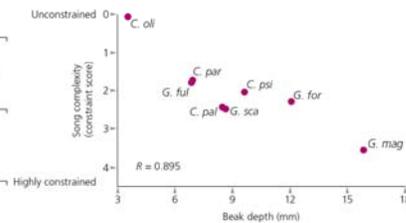
By random mating, the bird population can match the resource distribution.

Birds with extreme bill sizes (I & II) will have higher fitness, and assortative mating for bill size will be favored via **ecological selection acting indirectly** on mating traits.

(A-2a & b) Beak size and song phenotype in **Darwin's Finches**:
Bill size is a "magic trait" that **directly** affects both ecology and mate choice (Podos 2001, 2004; Herrel et al. 2009)



- Species with larger beaks have a more restricted vocal performance (greater 'vocal deviation'); that is, they have narrower frequency ranges and/or slower trill rates.
- The same is true **within** a species.
- Adaptation to different food niches changes the beak size, thus affecting **mate choice**, which is based on song.
- Ensures pleiotropy of ecology and assortative mating (**magic trait**)



• But the Grants (2006) aren't convinced!

Problems with some **continuous-resource** theoretical models: the so called “adaptive speciation” (adaptive dynamics) approach of Dieckmann and Doebeli -- 1999, 2005, etc.

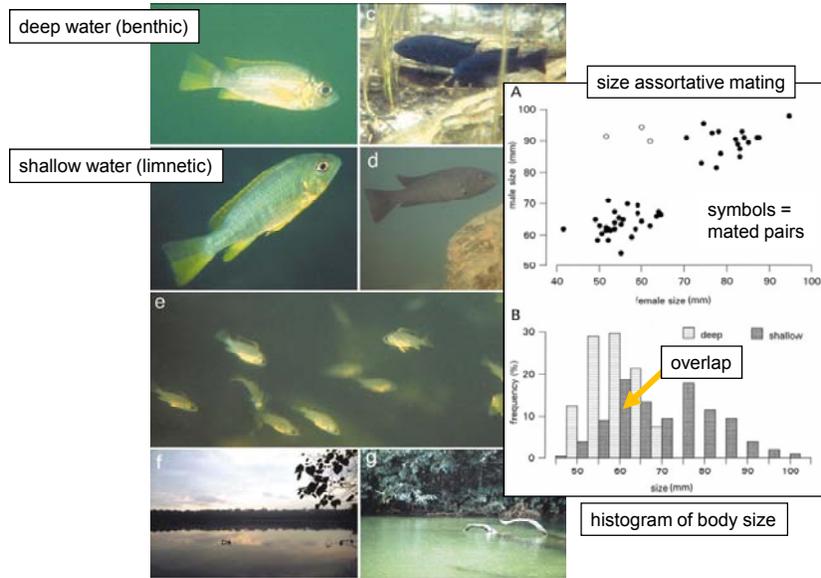
(critique by Waxman & Gavrillets 2005, Gavrillets 2005)

1. Initial genetic variation has the highest possible level (0.5, each allele)
2. Mutation rates are unrealistically high, by two orders of magnitude.
3. Neglect the **cost** of mate choice, while assuming strong choosiness:
 - Time spent searching for Mr. (or Mrs.) Right;
 - Exposure to predation while distracted;
 - Direct infliction of damage on females by males competing with one another.
4. Usually **require** the presence of “magic traits” to work well.

III. Examples from nature: Arctic Char trophic morphs in postglacial lakes:
Speciation via adaptation to alternative dietary resources
(Gislason et al. 1999; other lakes: Wilson et al. 2004)

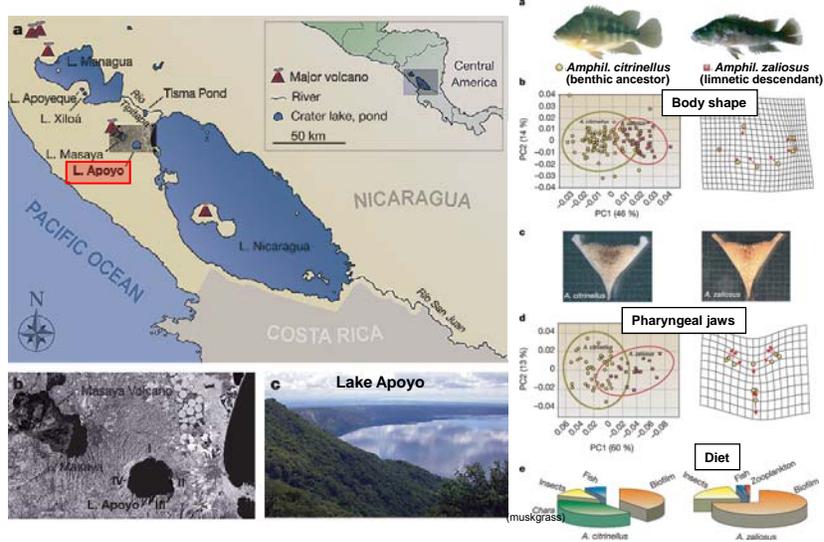


Example 2: *Tilapia* cichlid fishes in Lake Ejagham, Cameroon:
A monophyletic species pair (Schliewen et al. 2001)



Example 3: (<10,000 yrs): *Amphilophus* cichlid fishes
of the Midas group in a Nicaraguan lake

(Barluenga et al. 2006; Geiger et al. 2010; Muschick et al. 2011)



Note that reproductive isolation is complete: **no hybrids** in marker analyses

Example 4: “Speciation in a small place,”

Native palms of Lord Howe Island

(Savolainen et al. 2006; Babik et al. 2009)

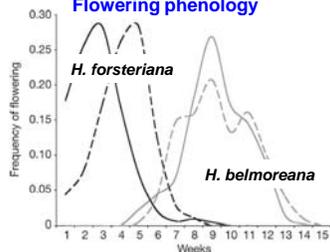


age =
6.9 my,
size =
16 km²

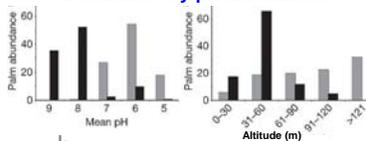
Kentia or thatch palm, *Howea forsteriana* (2N=32) Curly palm, (2N=32)

As many as 20 additional species have also arisen sympatrically here (Papadopoulos et al. '11, '13, '14; Coyne 2011)

Flowering phenology



Distribution by pH and altitude



AFLP genome scan for species differentiation shows few deviations from neutrality

