Hybrid speciation

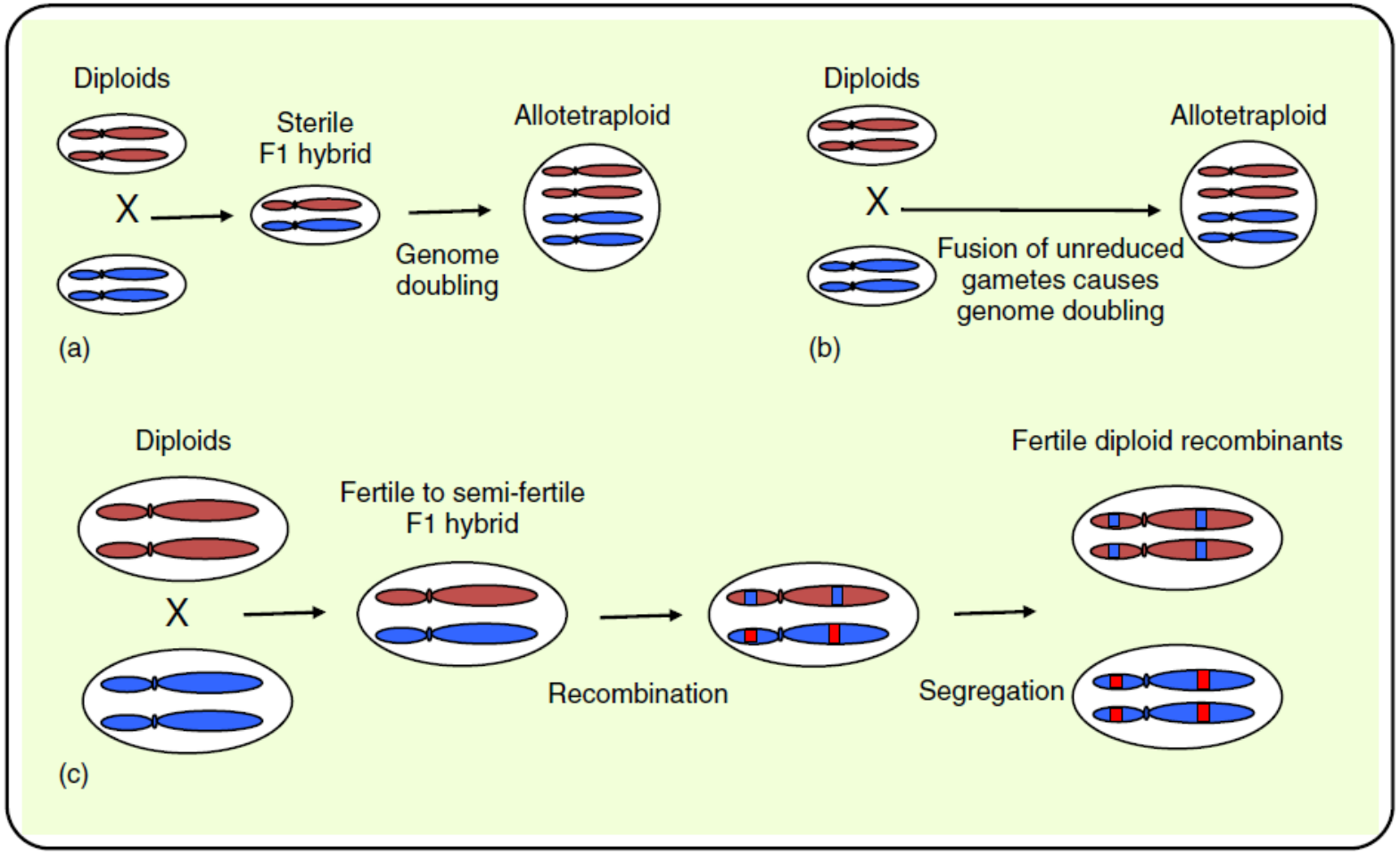
Hybrid speciation

Species are supposed to be reproductively isolated, so how on earth can you have hybridization between species that leads to speciation? Seems crazy!

And yet, we know that it does happen

What is “hybrid speciation?”

- In hybrid speciation, hybridization was important in the origin of a new species.
- In allopolyploid hybrid speciation, there’s ~50% from each parent, & the new species has RI
- In homoploid hybrid speciation (recombinational speciation), contribution of one parent may be much less, and reproductive isolation must presumably evolve, rather being immediately caused by the hybridization



What is NOT hybrid speciation?

- It surely isn't just a species that has undergone introgression from another species
- In "reinforcement", deleterious hybridization provides the force that leads to the evolution of reproductive isolation; but we wouldn't want to call that hybrid speciation either.
- "Despeciation" happens when pairs of species collapse due to hybridization (known from sticklebacks & cichlids in fish, and in Darwin's finches). But such swarms do not remain distinct from parents.
- Hybridogenetic species are hybrid species in a way, but that's a separate issue....

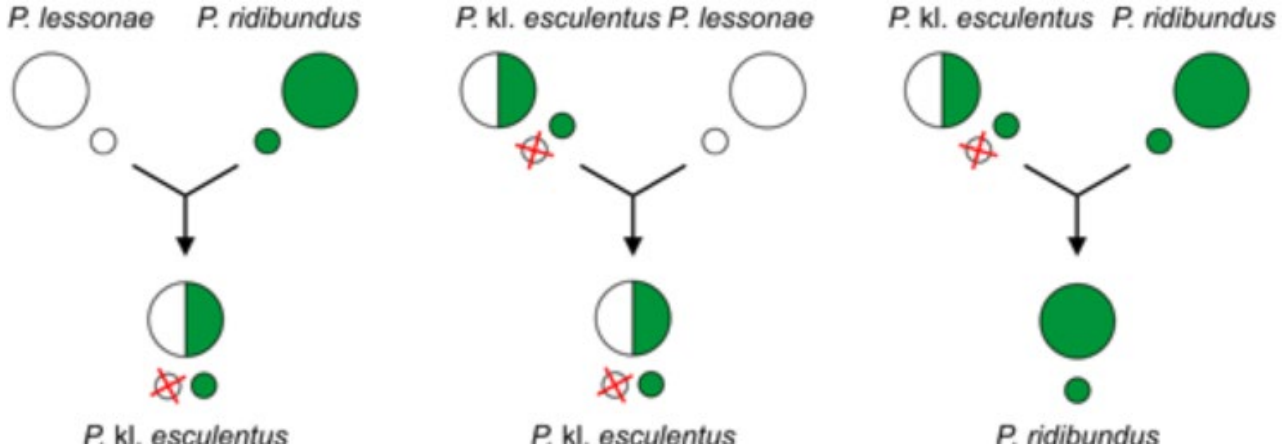
Hybridogenesis in European frogs

Pelophylax lessonae
The pool frog

*Pelophylax "*klepton" *esculentus*
The edible frog
Hybrid pool x marsh frog

Pelophylax ridibunda
The marsh frog

Hybridogenesis also occurs in some fishes and stick insects



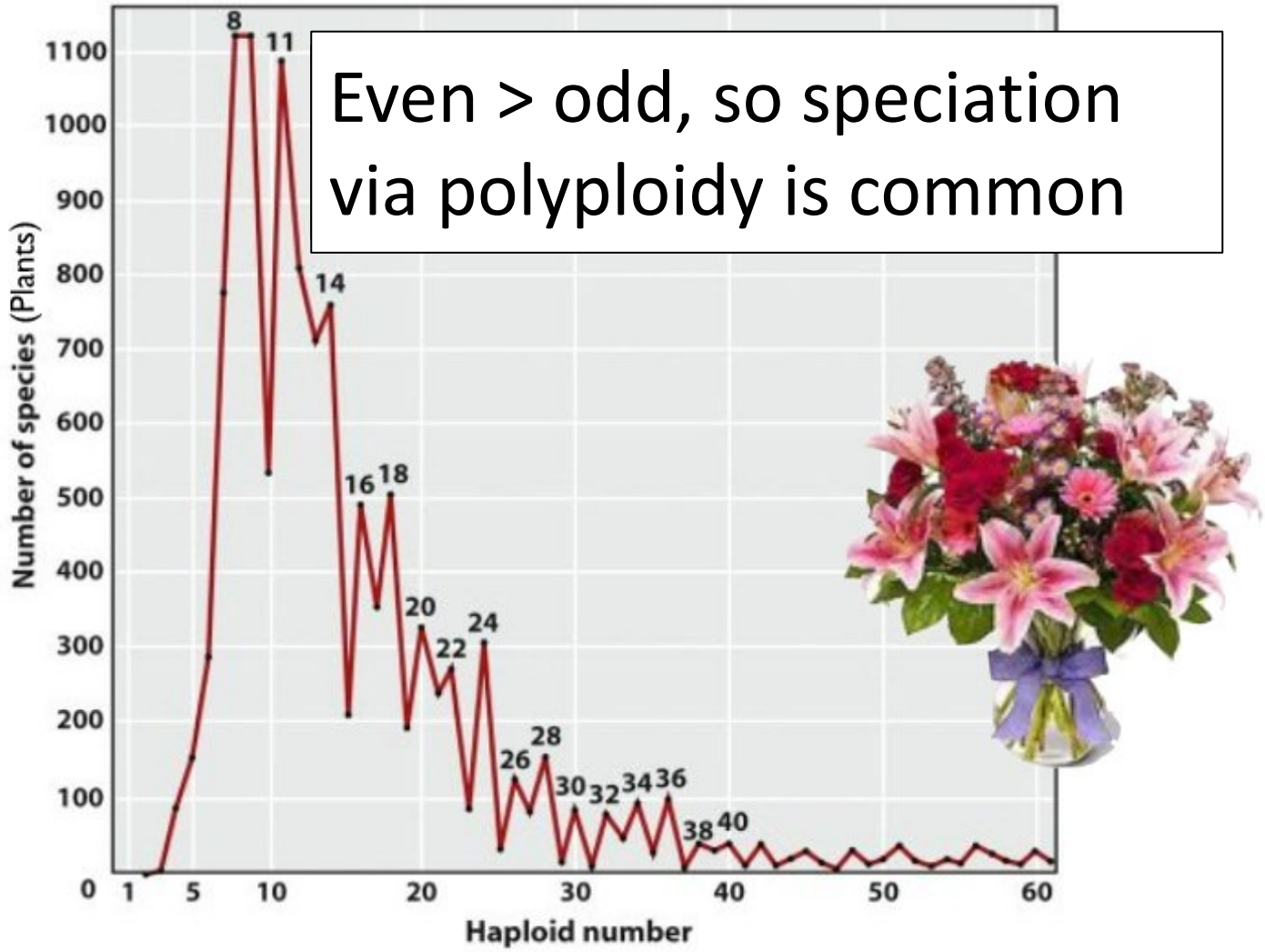
Male and female clonality; worker heterozygosity. *Paratrechina* ants

- The longhorn crazy ant! See Tseng et al. 2022, and Pearcy 2011.
- Males and females (queens) reproduce asexually.
- Hymenoptera (ants, wasps, and bees) are “haplo-diploid”. With haploid males and diploid females. Normally diploid females mate with haploid males to produce offspring of the same type.
- In *Paratrechina longicornis*, males are haploid, and are clones of their father.
- Queens are diploid, and are also produced clonally from their mothers.
- Workers are females, but do not reproduce. They are produced sexually due to mating by a queen and a male.

So what IS hybrid speciation?

- Abbott & Rieseberg 2021 (and earlier, I think): “Hybridisation between genetically divergent populations may lead to the formation of new evolutionary lineages”
- Mallet 2007: “...I here restrict the term to cases where hybrid allelic combinations contribute to the spread and maintenance of stabilized hybrid lineages generally recognized as species.” [Species are clusters of genotypes stable in sympatry]. Mallet pointed out that many supposed “hybrid species” do not coexist with both parents.
- Schumer et al. 2014: Hybrid speciation rarer than hitherto assumed:
  - “The key shortcoming in most studies proposing hybrid speciation is the lack of evidence that hybridization played a role in the speciation process”

Frequencies of chromosome number



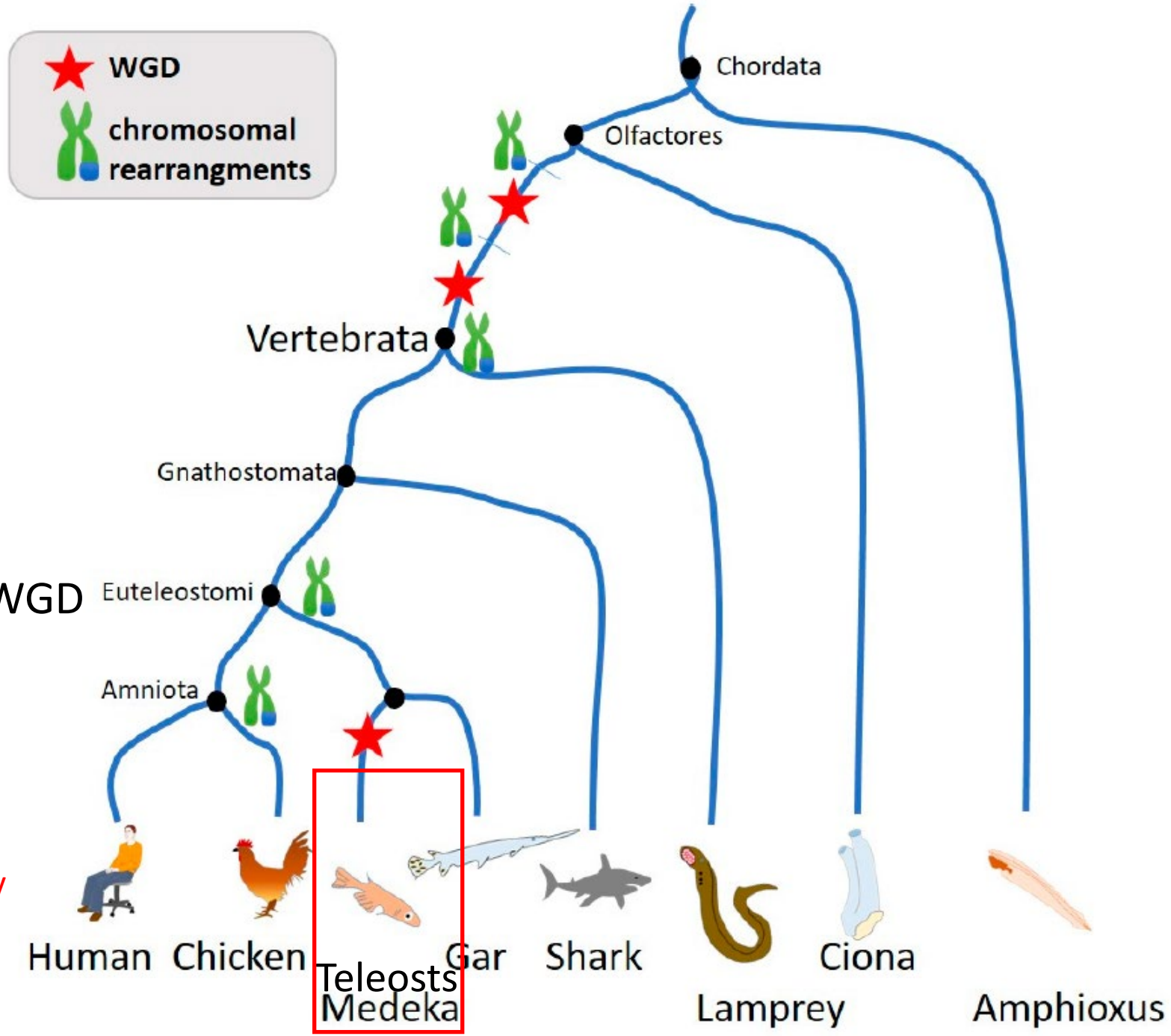
- But no saw-tooth graph in animals

Chromosome doubling in vertebrates

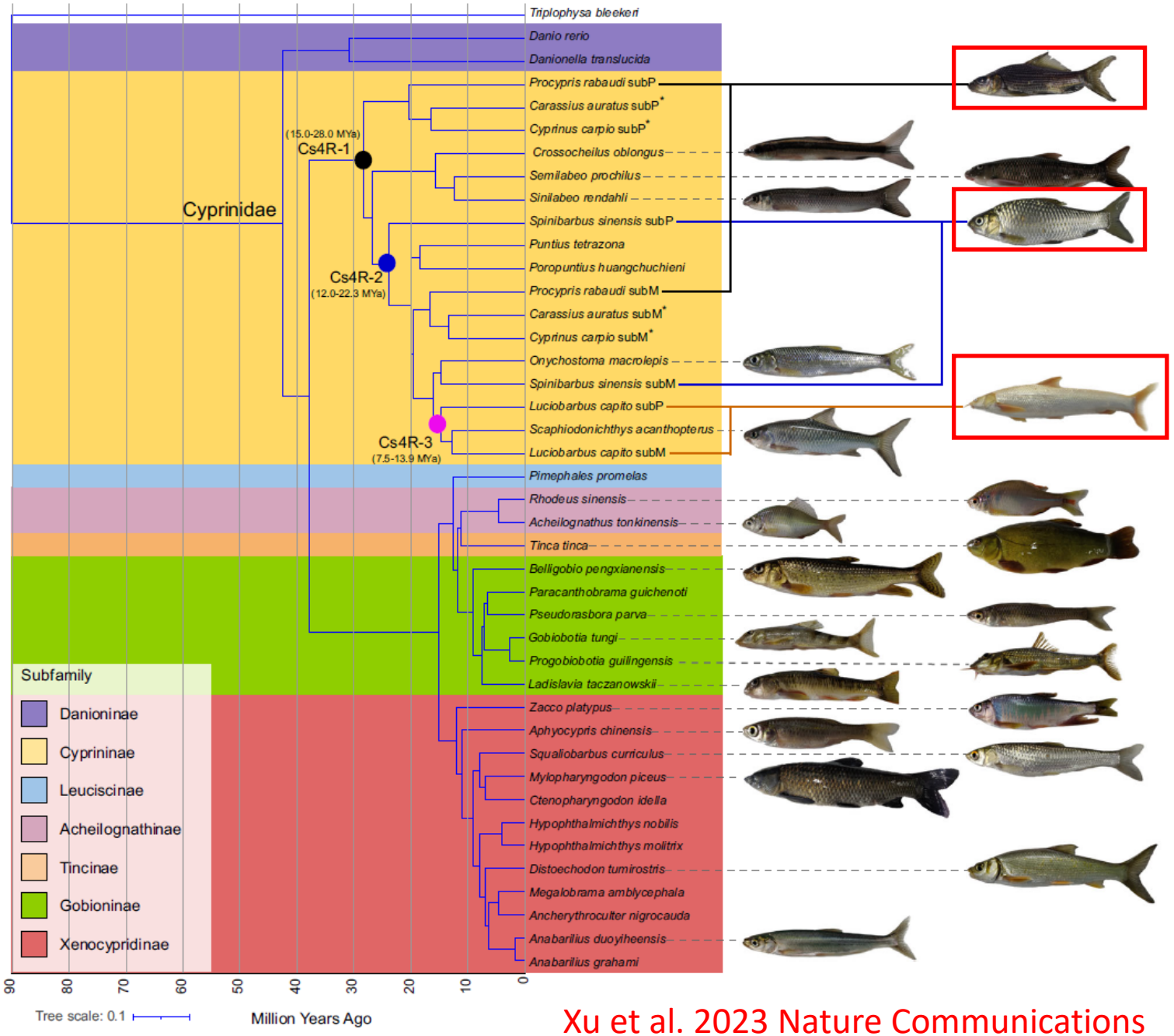
Whole genome doubling (★WGD)

= a lot more local WGD going on here!

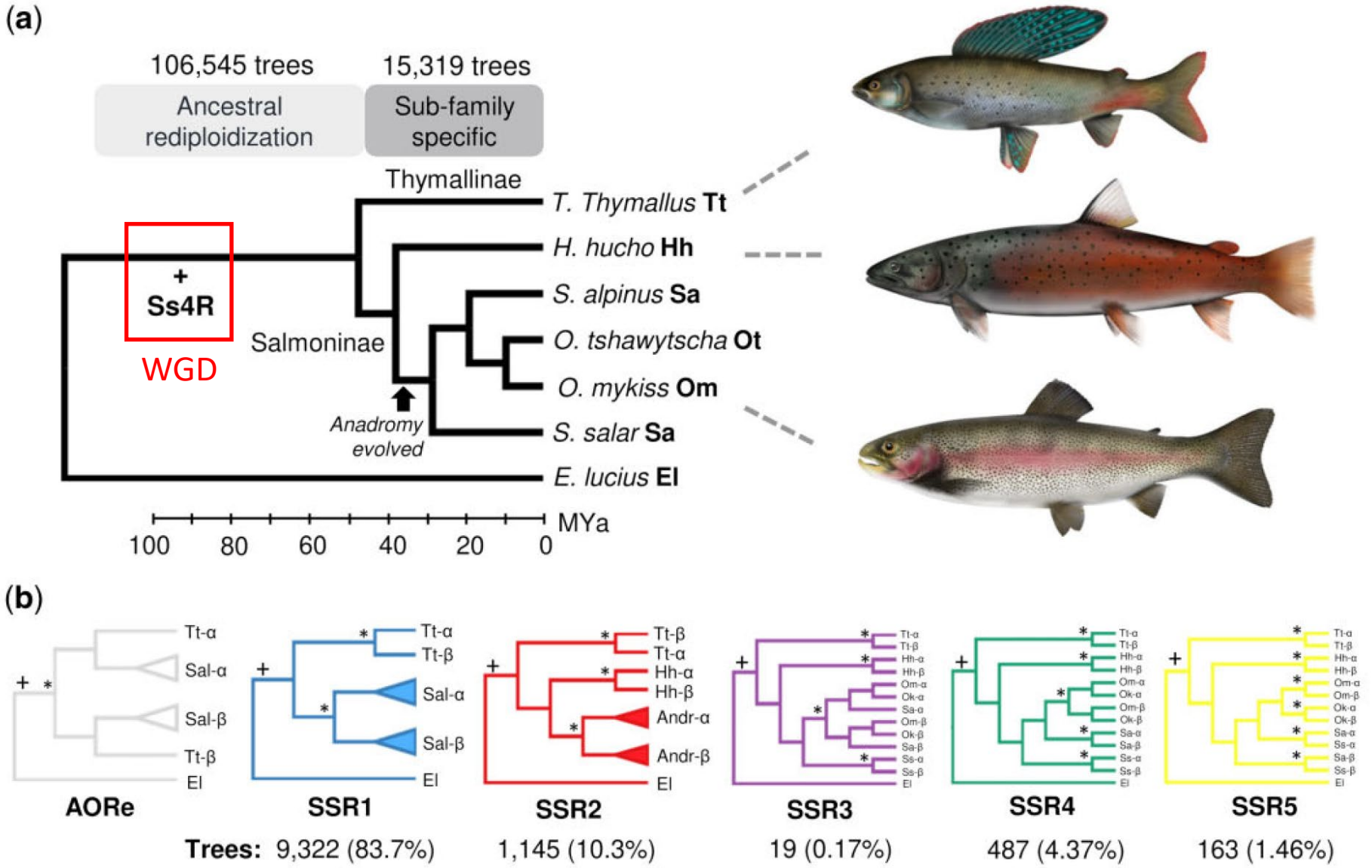
Sacerdot et al. 2018. Genome Biology
Comaills & Castellano-Pozo 2023. Biology



Allopolyploid origins of perches and goldfish species



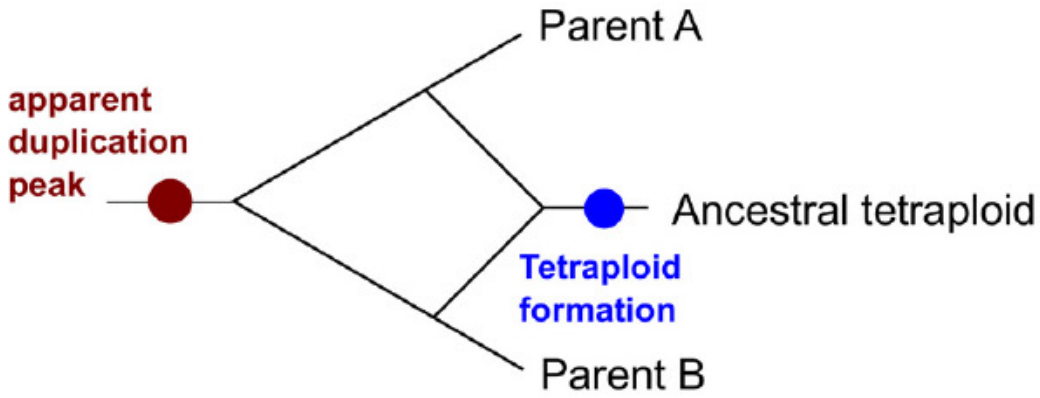
Xu et al. 2023 Nature Communications

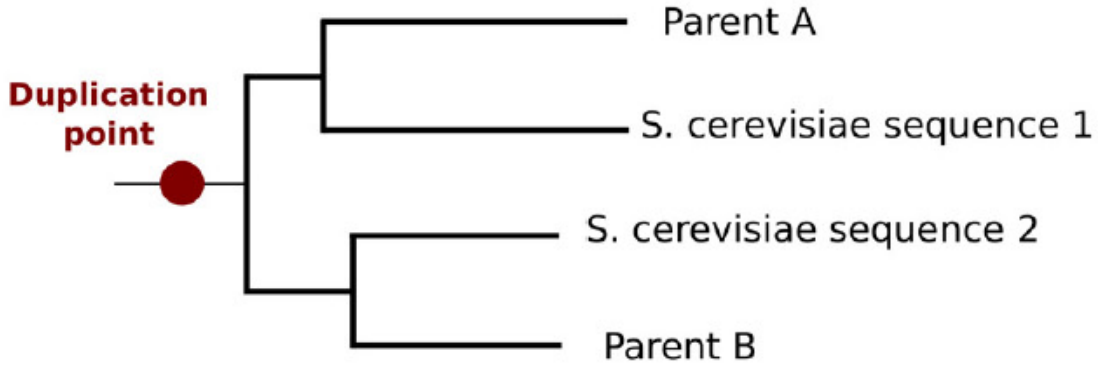


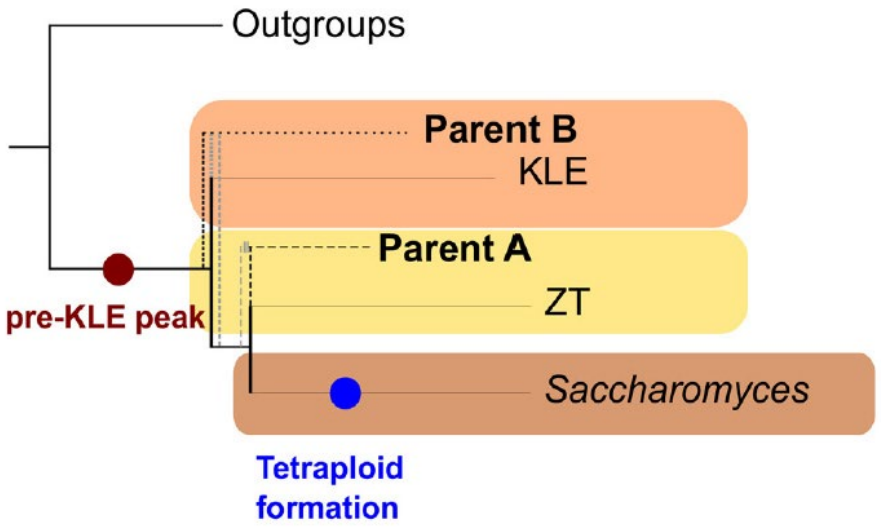
Gundappa et al. 2022. Molec Biol Evol.

"Although the possibility of segmental allopolyploidy cannot be excluded, it is likely that the salmonid genome was doubled through autopolyploidy."
Allendorf & Thorgaard 1984. In B.J. Turner, ed. Evolutionary Genetics of Fishes.

Saccharomyces allopolyploid lineage, 135 Mya







Marcet-Houben, M., & Gabaldón, T. 2015. PLoS Biology 13:e1002220.

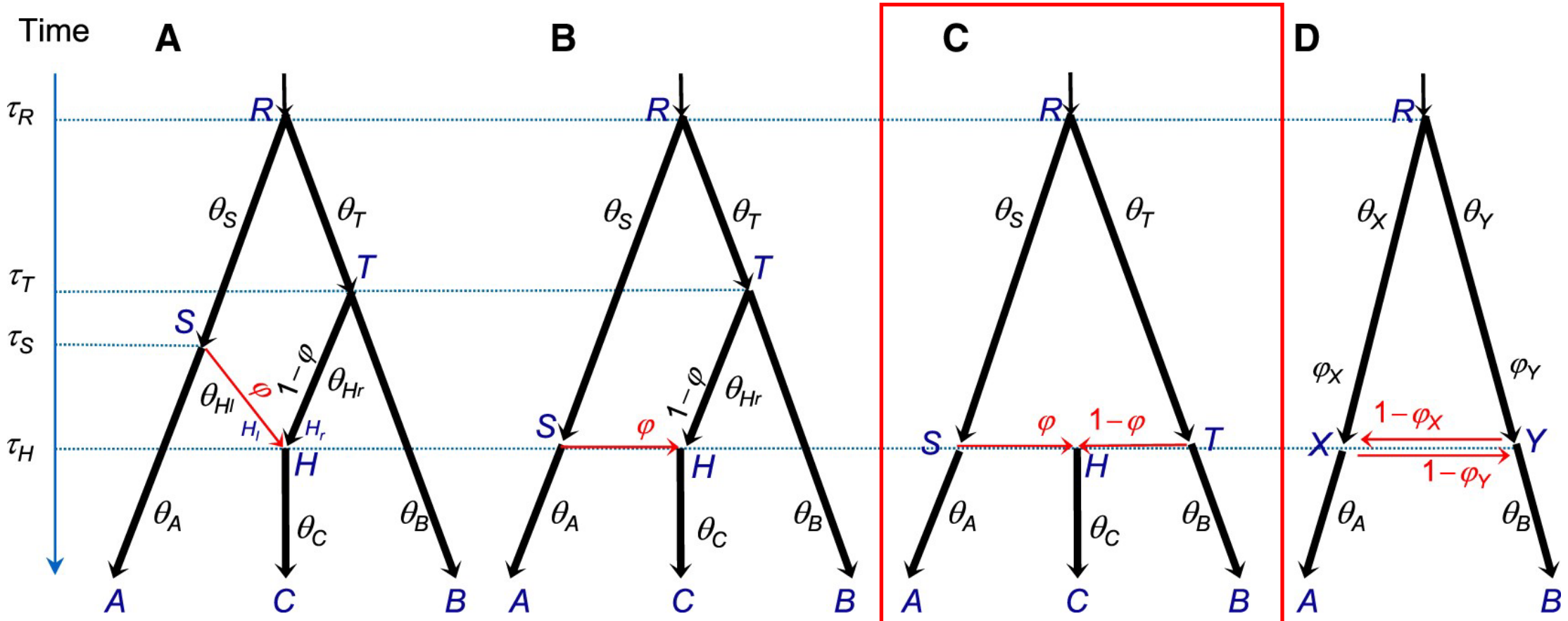
Hybrid species: homoploid hybrid speciation

Hybridization led to the origin of a new species without chromosome doubling.

Typically, early generation hybrids will be less isolated from parent species than the parent species are from each other.

It is envisaged that, sometimes, from the great variation induced by hybridization and crossing by the hybrids with parents and with each other, new reproductively isolated species can be selected out.

Hybrid speciation and the multispecies coalescent



Introgression from a "ghost species"

Introgression

Homoploid hybrid speciation

Bidirectional introgression

Flouri et al. 2020. Mol. Biol. Evol. 37: 1211-1223

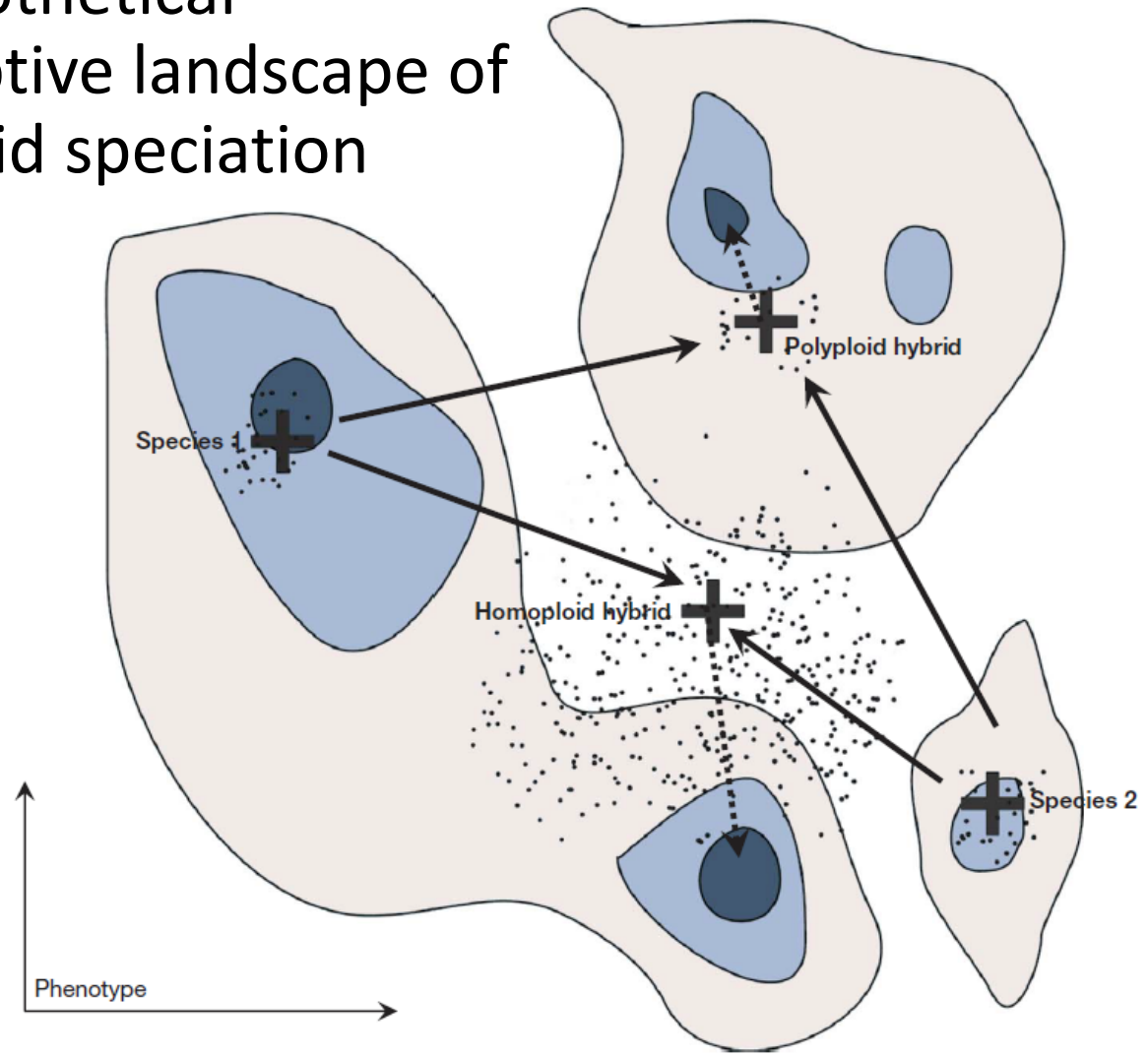
Hybrid speciation seems unlikely

A new hybrid seems like a “hopeful monster” (Goldschmidt’s term)!

Also, if species are reproductively isolated, how could a hybrid become reproductively isolated from both parents?

Homoploid hybrid species: “transgressive variation” in quantitative traits: + + + – – and – – – + + genotypes can hybridize to produce – – – – – and + + + + + transgressive variants

Hypothetical adaptive landscape of hybrid speciation



Homoploid hybrid speciation: sunflowers

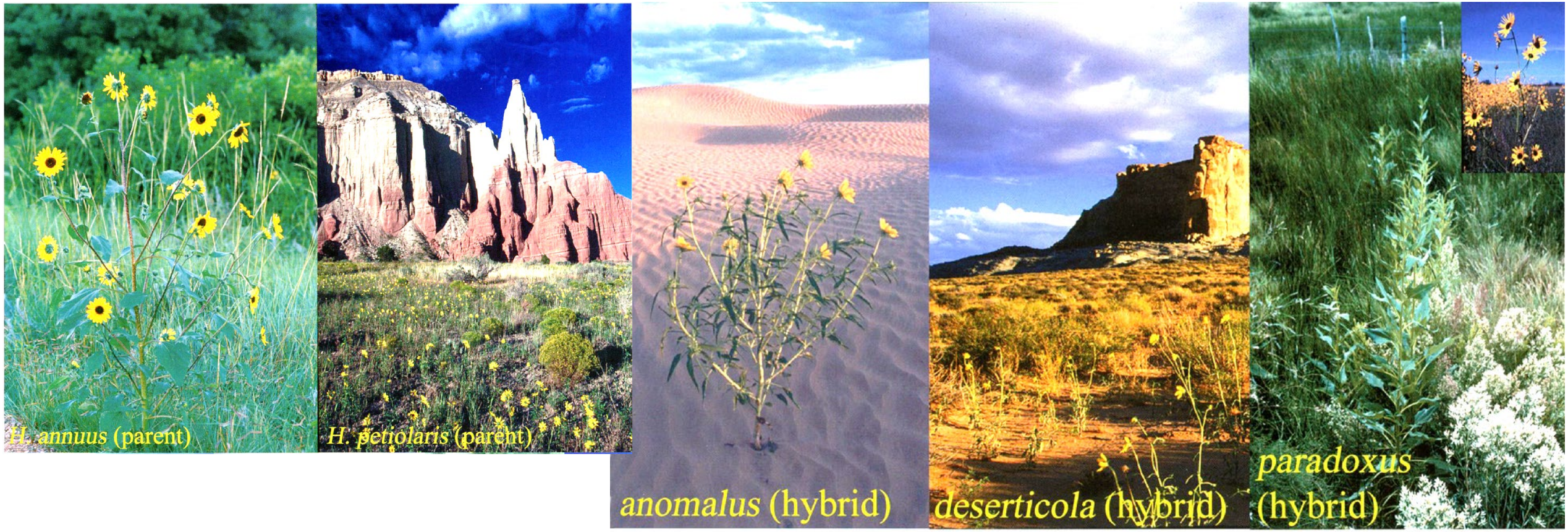
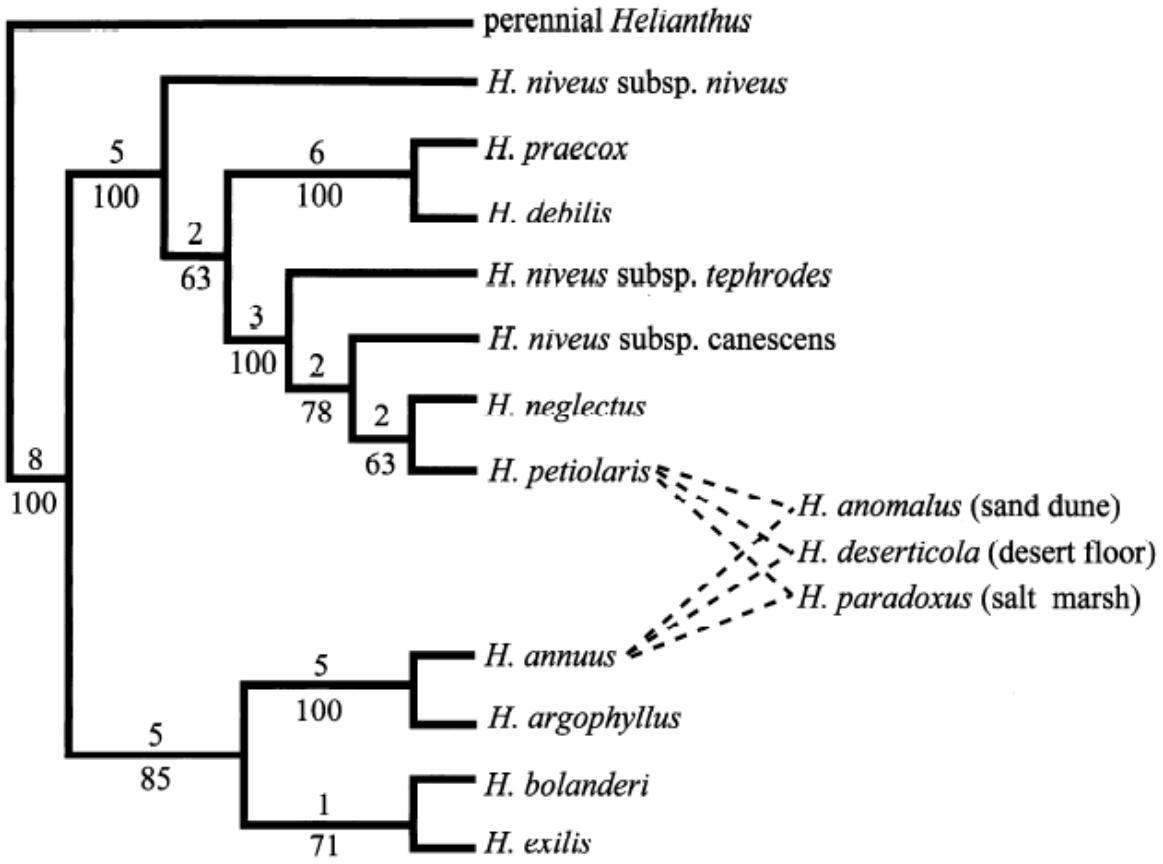


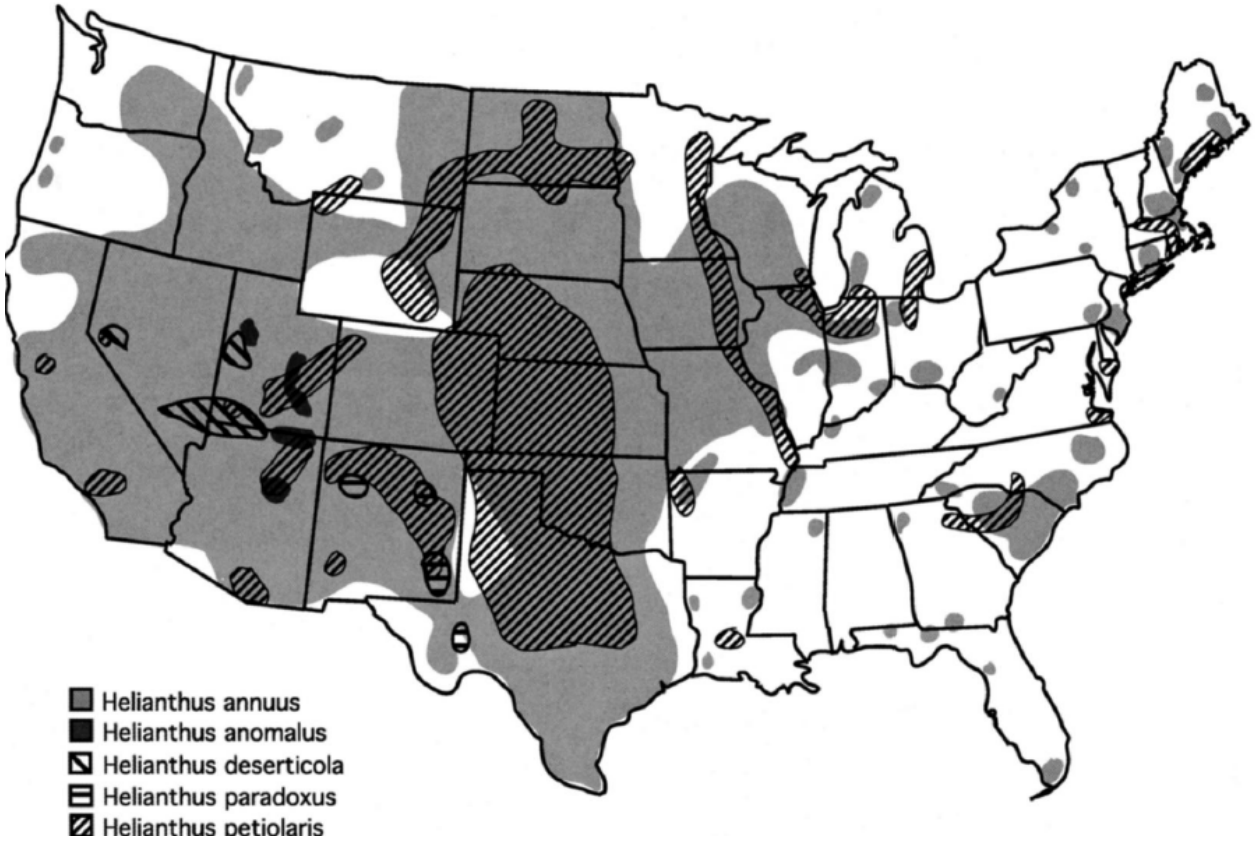
Figure 3. Photographs of the two parental species and their three hybrid derivative species in typical habitats. Photographs by Jason Rick.

Rieseberg 2006

Homoploid hybrid speciation

For example: in sunflowers, *Helianthus* species, studied by Loren Rieseberg and colleagues since the 1990s





Rieseberg 2006

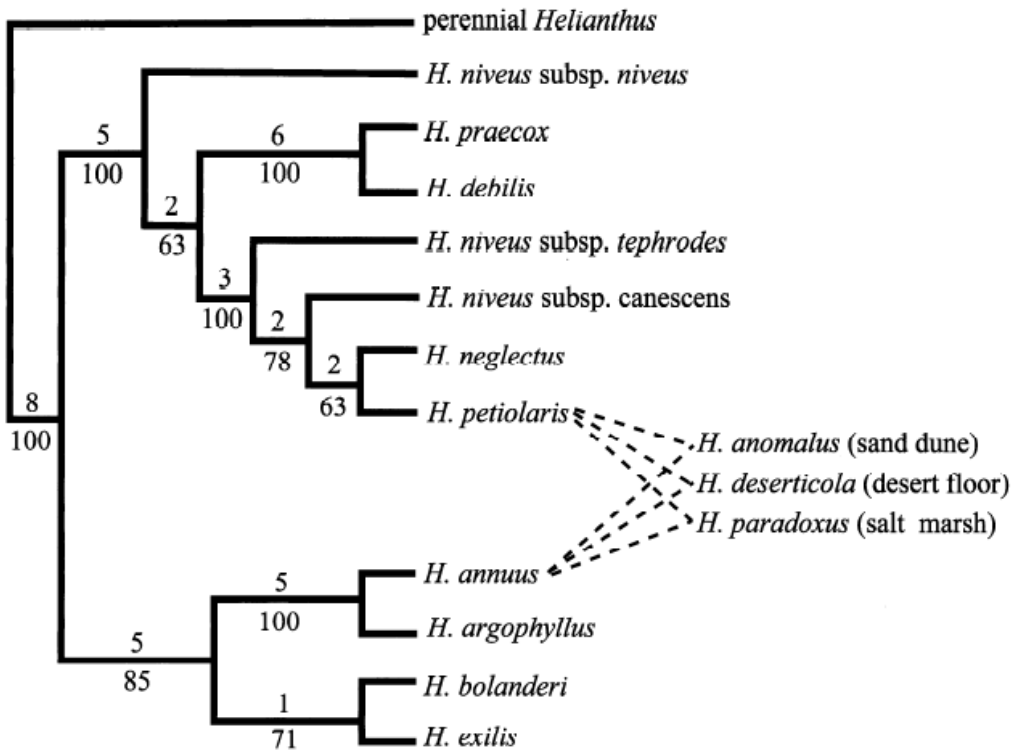
Homoploid hybrid speciation in *Helianthus*

- *Helianthus annuus* and *H. petiolaris* do hybridize naturally
- *Helianthus annuus* still hybridizes with each of the putative hybrid species
- Each hybrid species has a unique combination of chromosomal rearrangements. Also total of 3 (H. anomalus), 2 (deserticola) and 5 (paradoxus) translocations required, and about ~50% of the barrier between the species is caused by these rearrangements.
- Synthetic hybrid swarms repeatedly stabilize with rearrangement combinations similar to those in the natural hybrid species and are more compatible with hybrid species than parental species.
- Synthetic hybrids show transgressive variation in morphological and ecophysiological traits

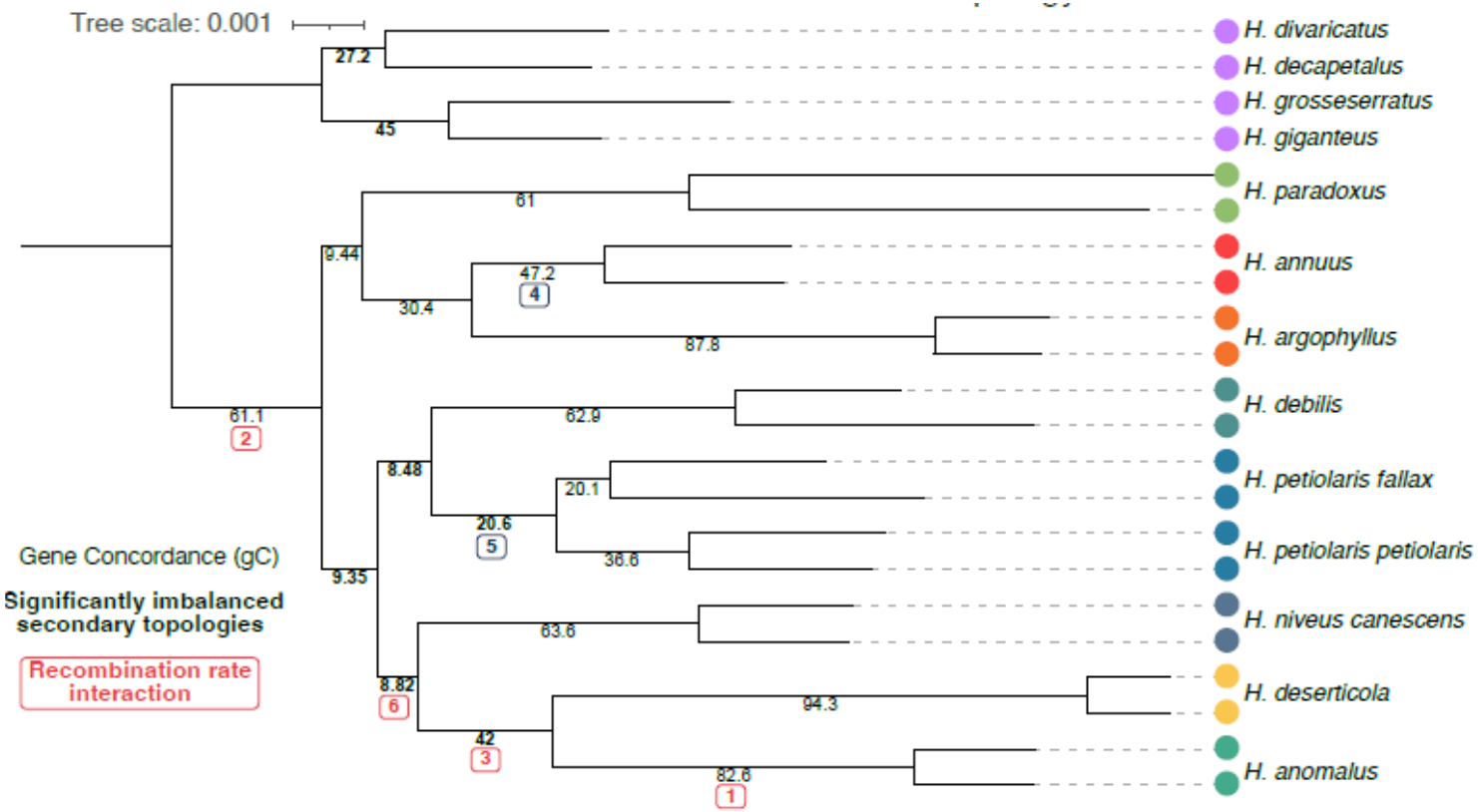
Rieseberg 2006

Helianthus hybrid speciation? Genomics

Prior hypothesis

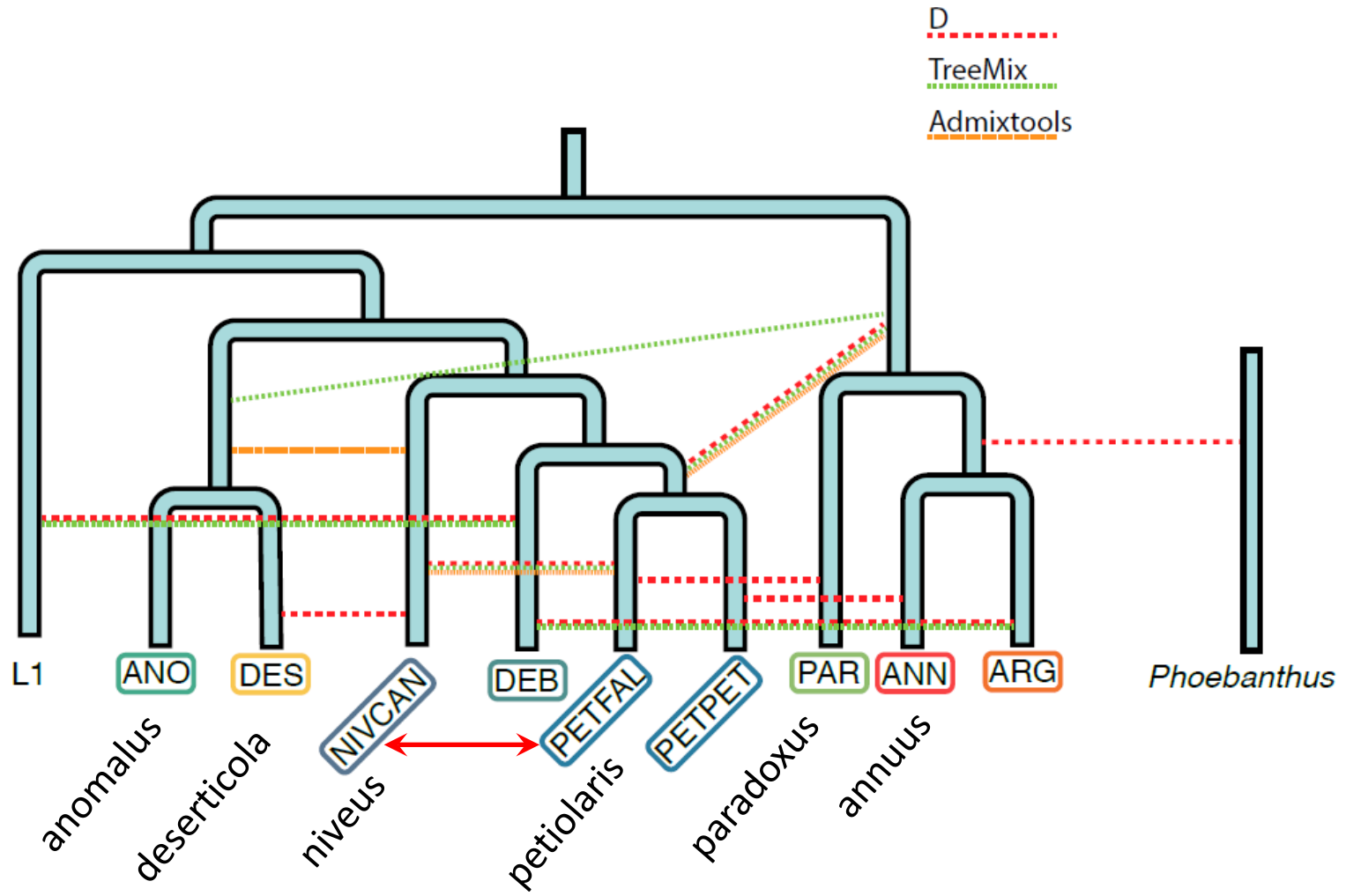


Maximum likelihood concatenated topology
(same as ASTRAL coalescent-aware topology)



Owens et al. 2022 BioRxiv

Helianthus hybrid speciation? Genomics



" ...admixture has been common in *Helianthus* throughout its evolutionary history, and that it has had a profound effect on phylogenomic relationships in the genus ...

Whether these ancient hybridization events triggered diversification ... remains unclear"

H. petiolaris fallax, used in previous experimental studies, was taken from a hybrid zone with *H. niveus canescens*, where the two species are indistinguishable!

Owens et al. 2022 BioRxiv

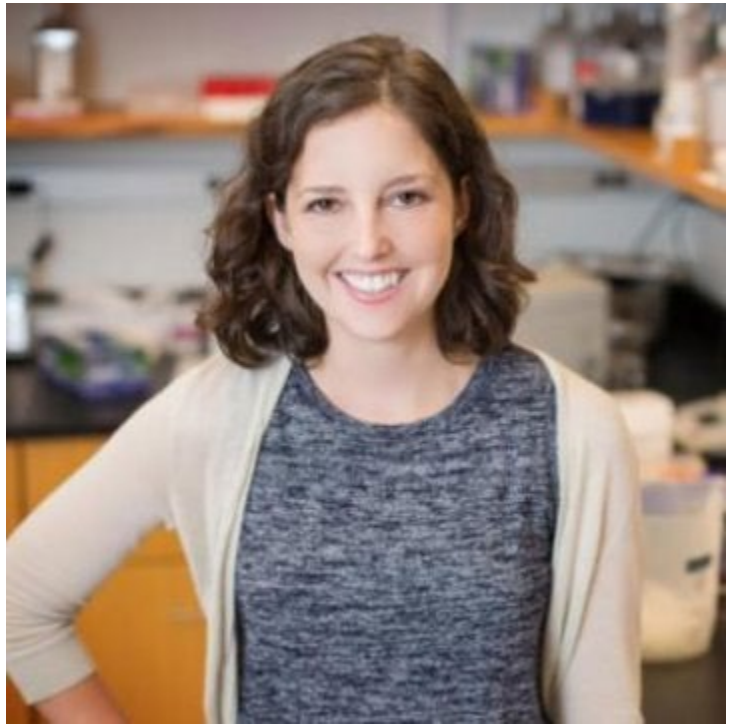
The Molly Schumer et al. criteria and hybrid speciation

Schumer et al. 2014: Hybrid speciation rarer than hitherto assumed: “three criteria must be satisfied:”

(1) reproductive isolation of hybrid lineages from the parental species,

(2) evidence of hybridization in the genome, and

(3) evidence that this reproductive isolation is a consequence of hybridization

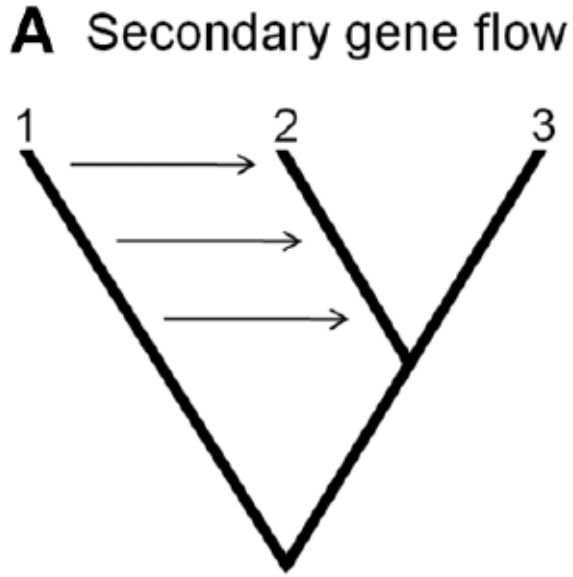


Schumer et al. 2014 provide helpful picture

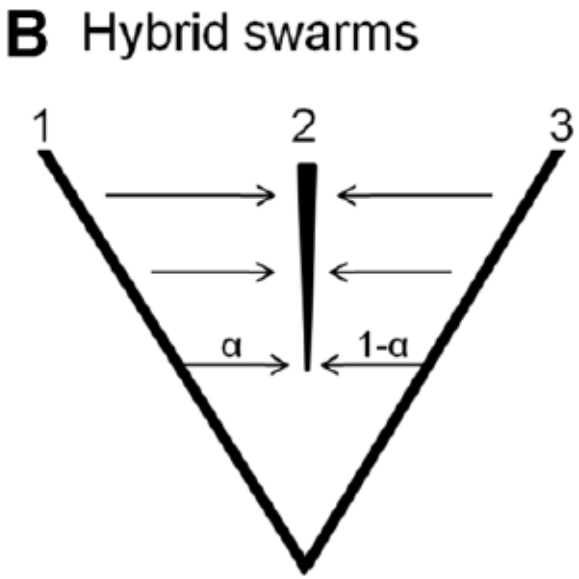
Criteria:

1. Reproductive isolation
2. Hybridization
3. Hybridization directly involved in reproductive isolation

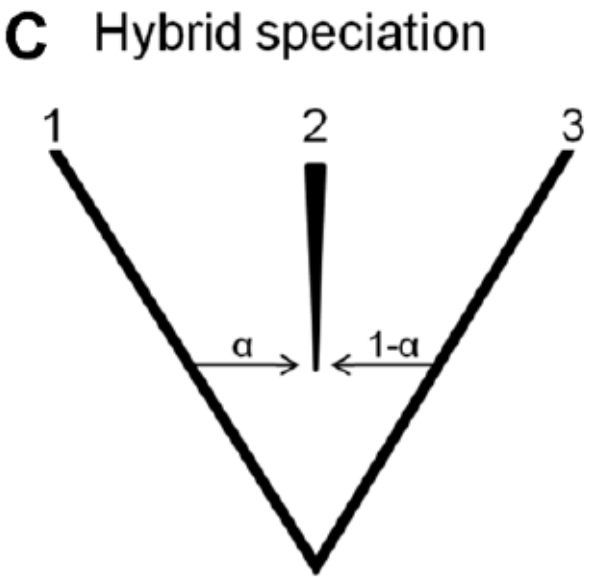
Criteria seem strict! Feliner et al. 2017 Heredity; answered by Schumer et al. 2018 Heredity.



Criteria 1 and 2 met, but not 3



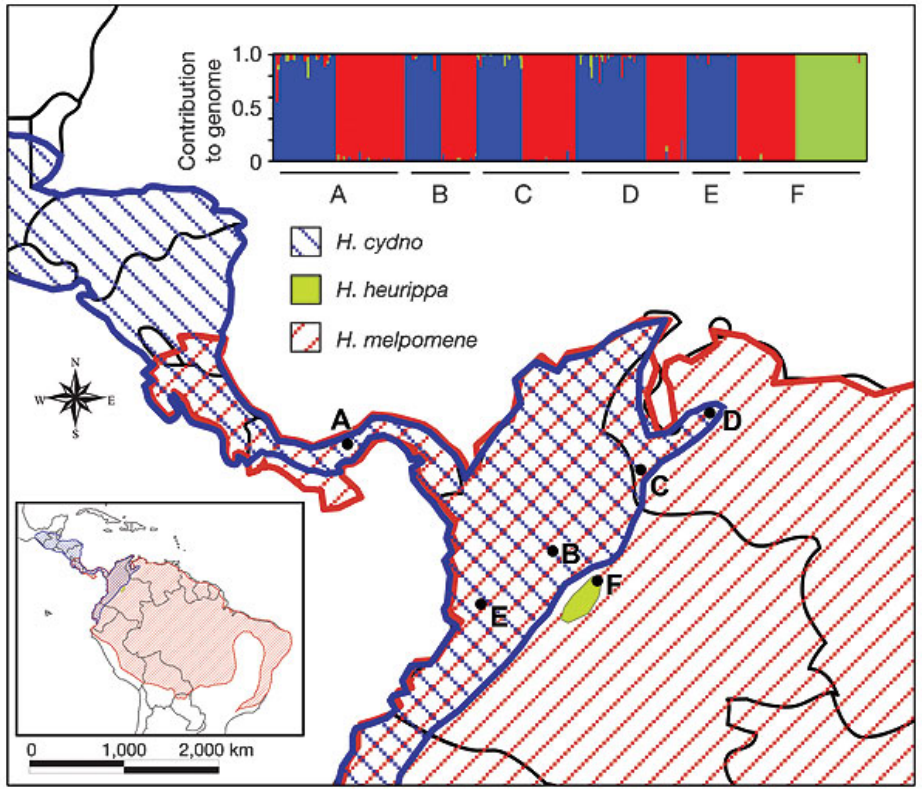
"Despeciation": Criteria 2 met, but not 1,3



Criteria 1, 2 and 3 all met

Homoploid hybrid species

Example from animals: *Heliconius* butterflies *Heliconius cydno* x *H. melpomene*
Hybrids show Haldane's Rule, but males are fertile. Some of these inferred to have backcrossed to produce a homoploid hybrid species that now coexists with *H. melpomene*



Colour pattern differentiation and assortative mating (preference) occur together!

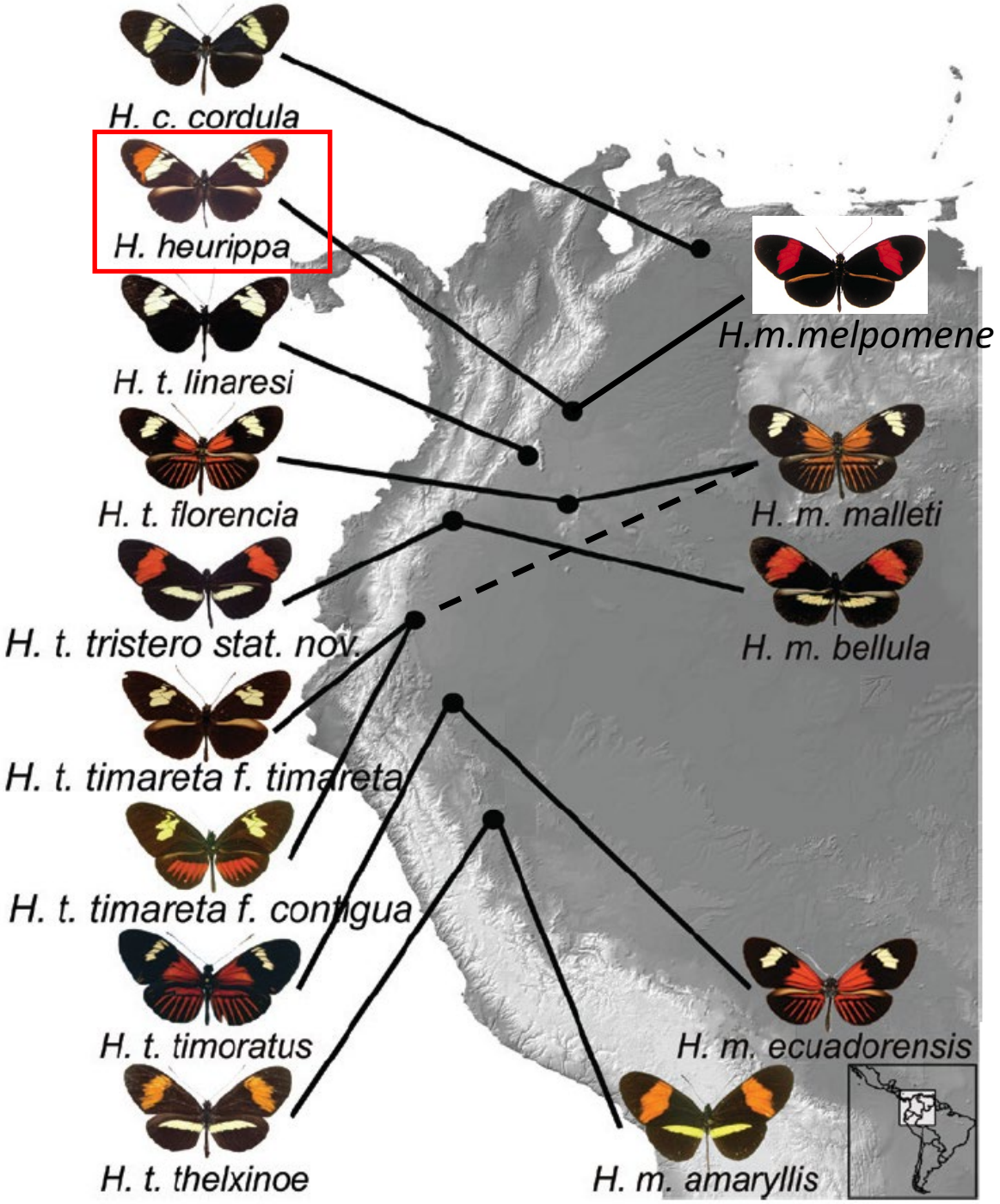
Mavarez et al. 2006

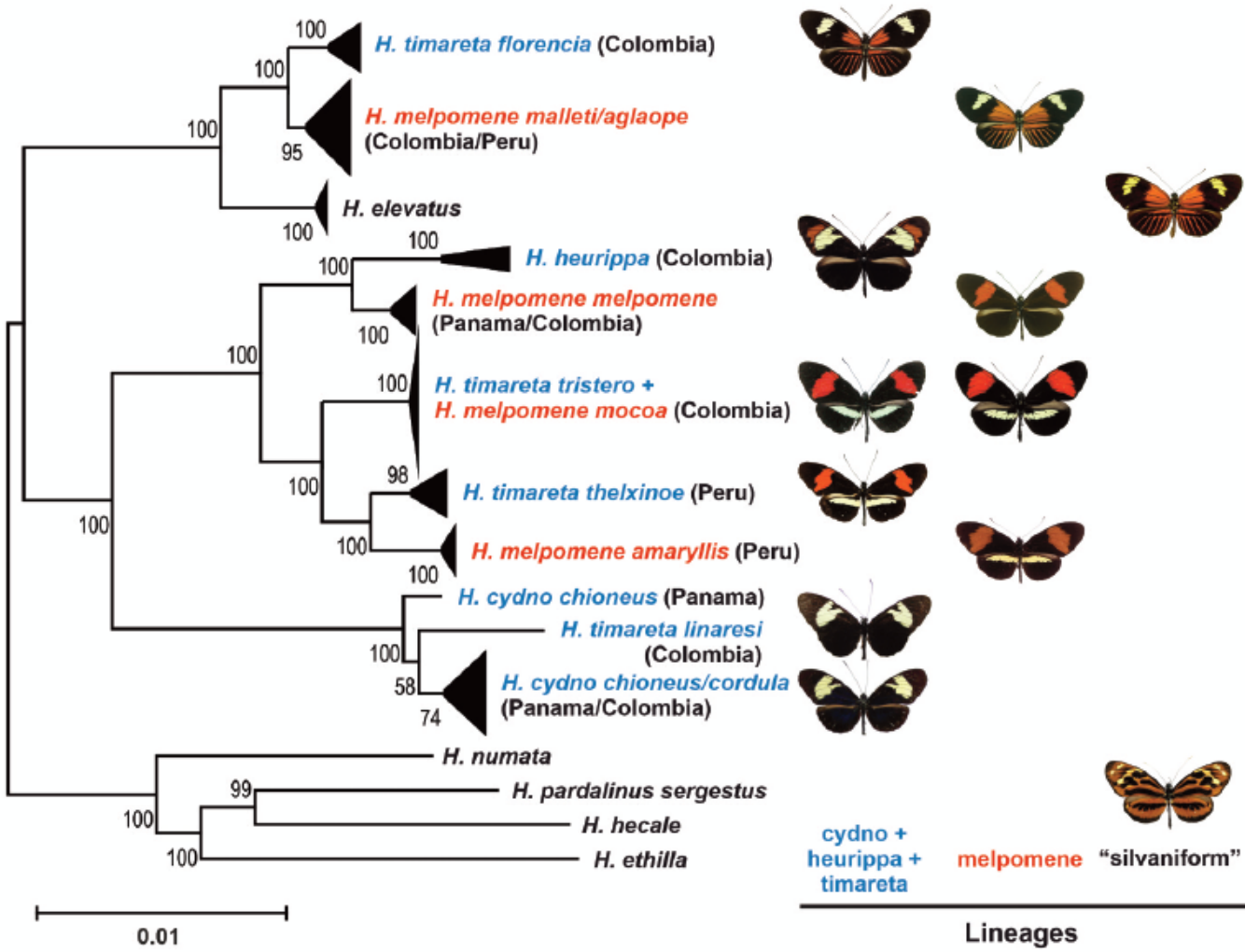
Schumer et al.: Hybrid speciation

- Good examples from *Helianthus* (according to Schumer et al.)
  - *Now known to be at least partially incorrect*
- "The best-supported case of hybrid speciation in animals comes from butterflies". *Heliconius heurippa.*
  - Artificial hybrids recreate the colour pattern
  - There's evidence for gene flow between *H. cydno* and *H. melpomene* in sympatry
  - The colour pattern provides some strong mating isolation from *Heliconius melpomene*, and weaker evidence of mating isolation with *H. cydno*
  - What about recent evidence? *Unfortunately, probably not a "hybrid species"*

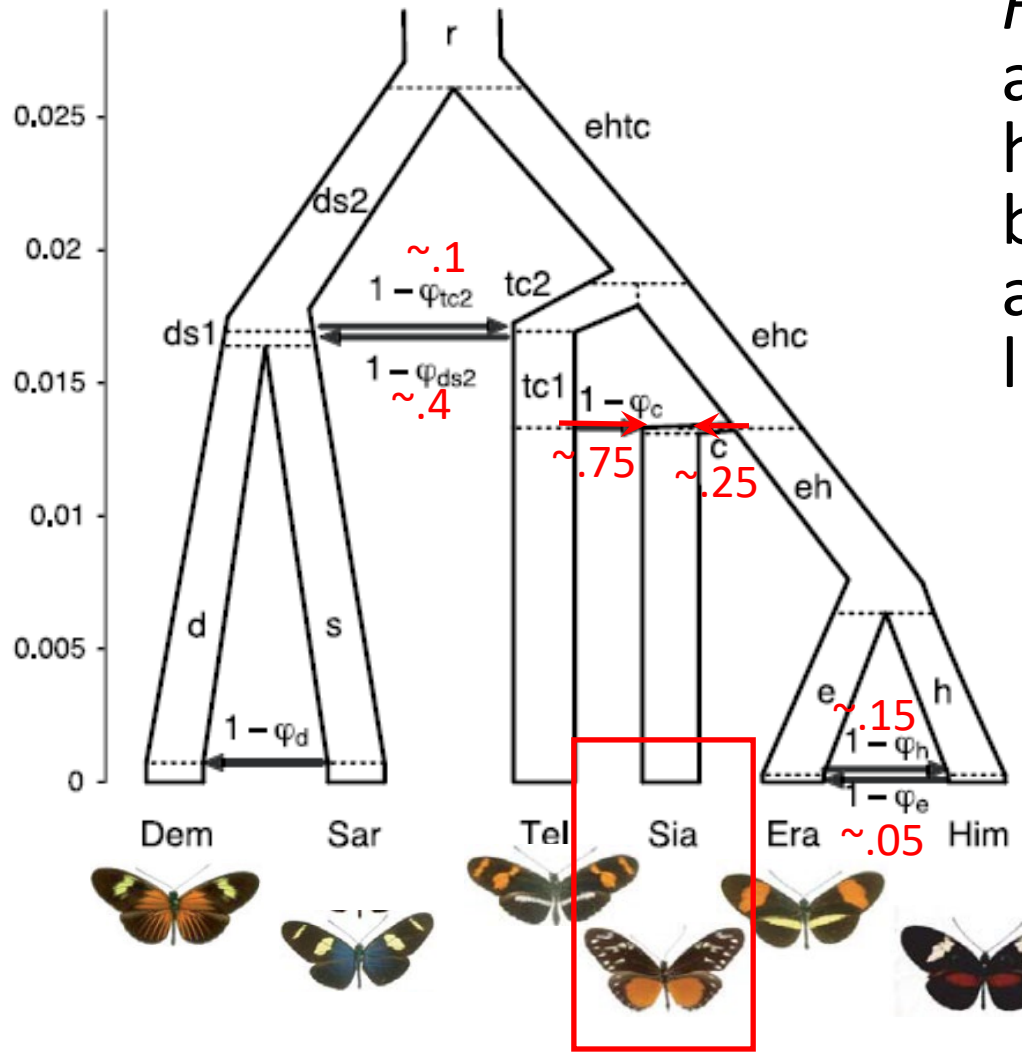
Schumer et al. 2014

H. heurippa as a hybrid species: maybe not so well supported after all?





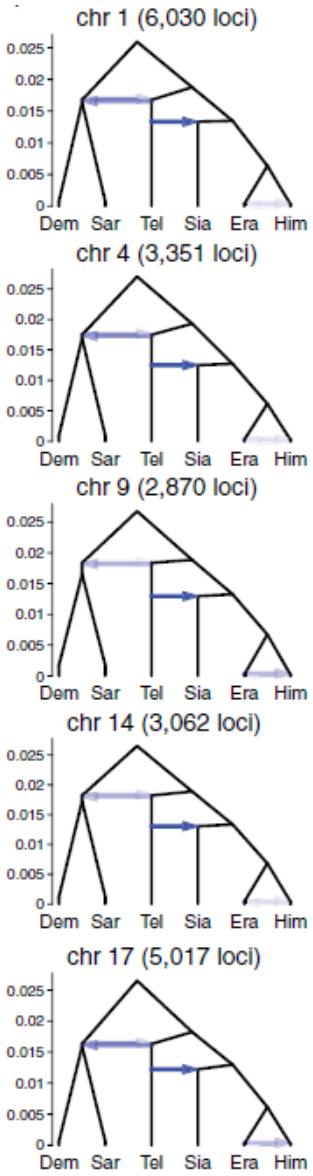
But we've discovered some new hybrid species in *Heliconius*, now!



Heliconius hecalesia appears to be an old hybrid species between *H. erato* and *H. telesiphe* lineages

The coalescent-based signal is rather consistent across the genome

Neil Rosser also has another example!



Homoploid hybrid species in *Ostryopsis* (Betulaceae)

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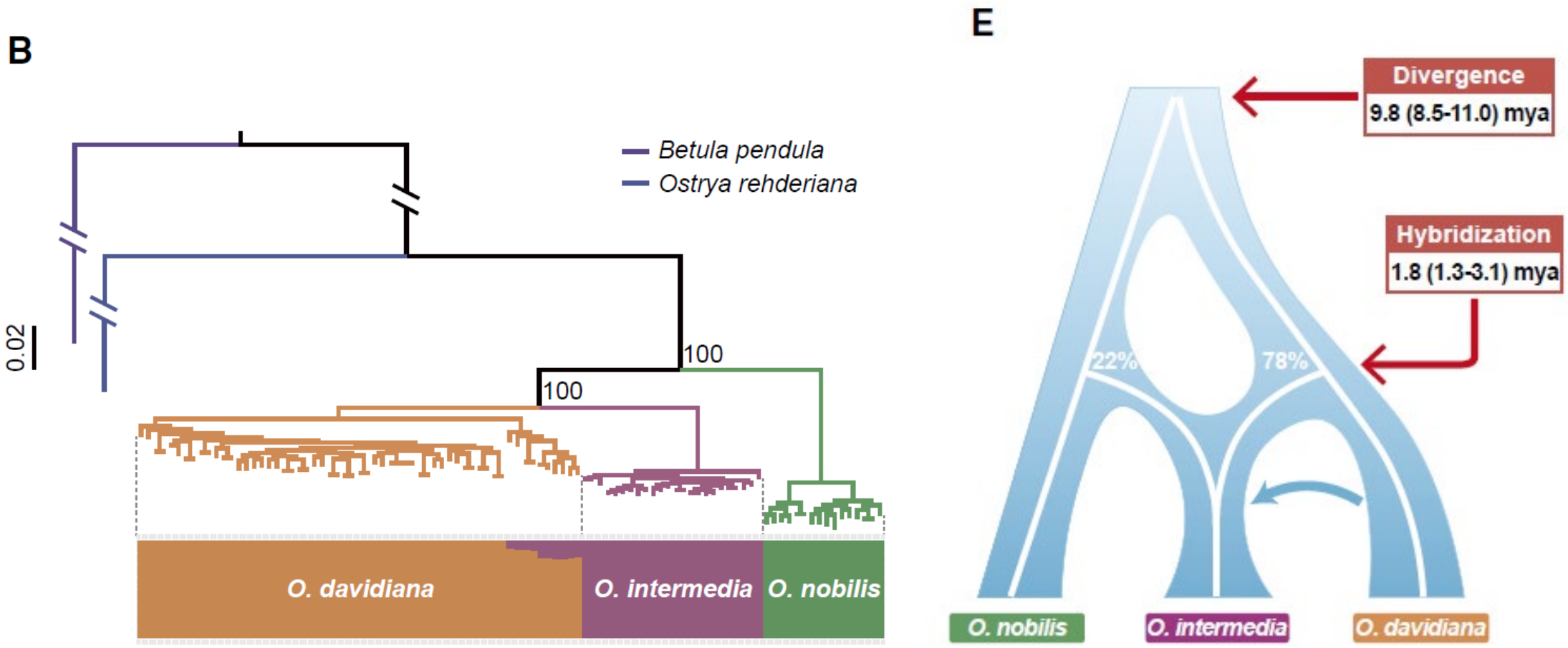
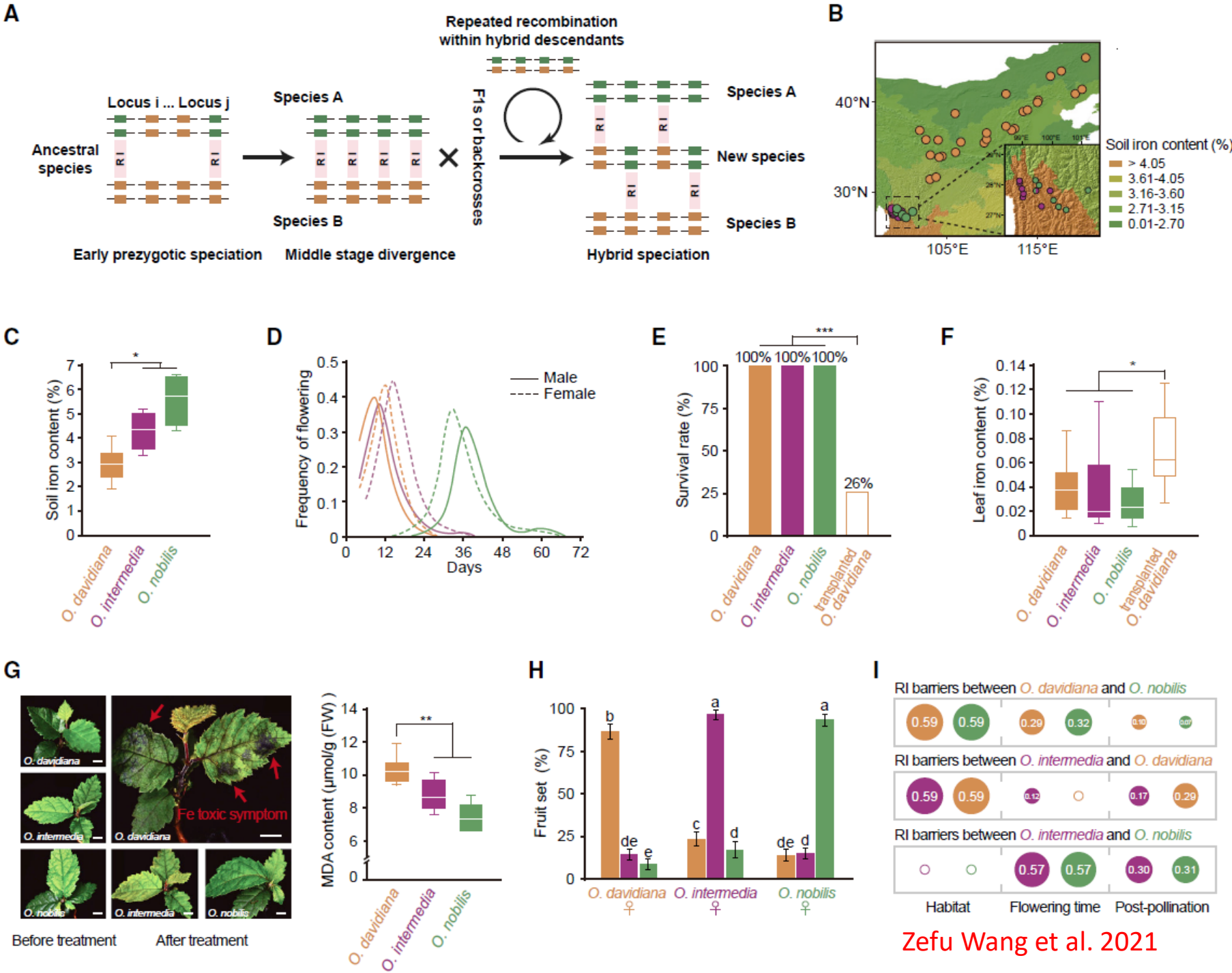


Zefu Wang et al. 2021

Homoploid hybrid species in *Ostryopsis* (Betulaceae)

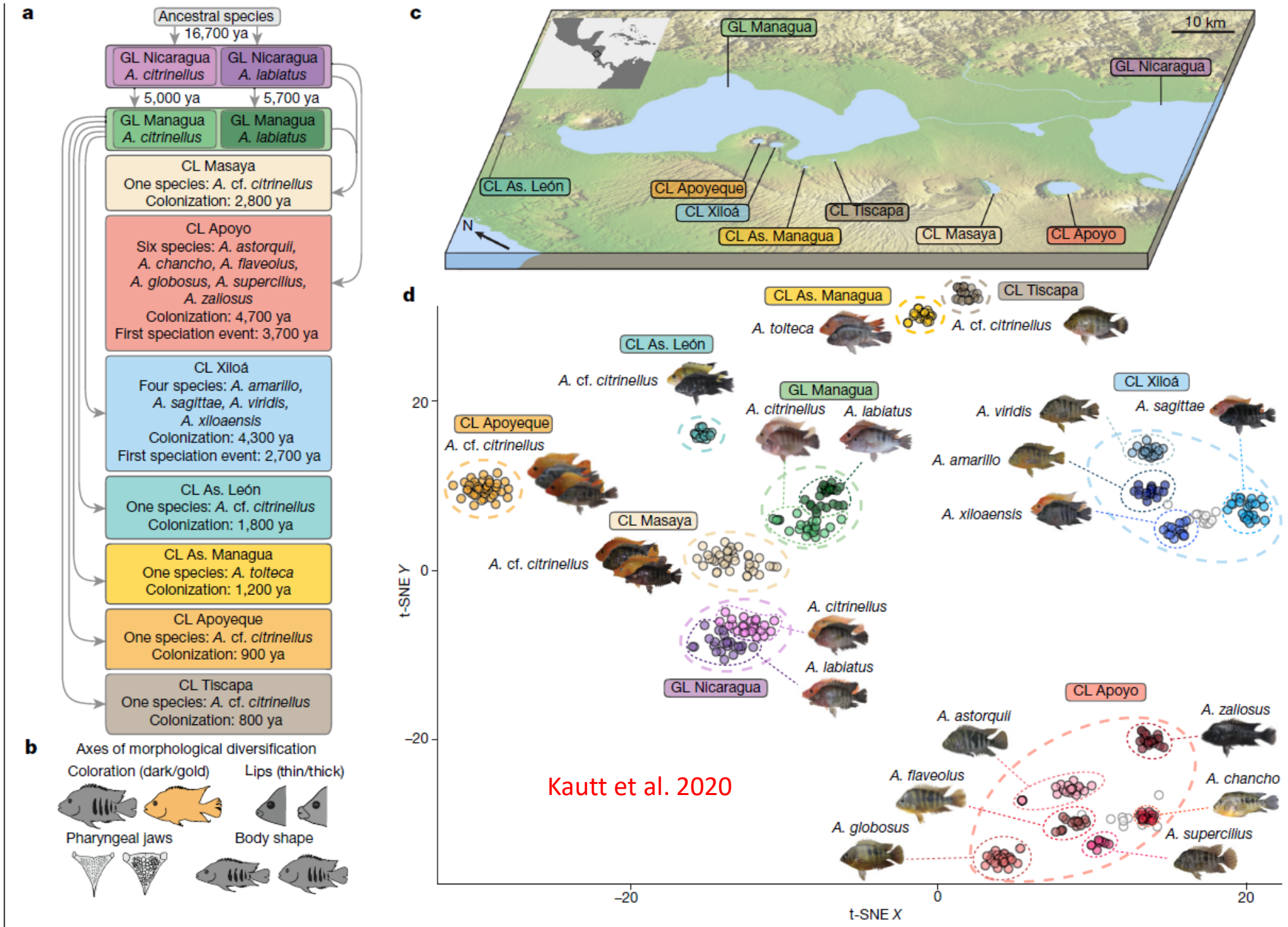
Something is also known about the genetics of the differences



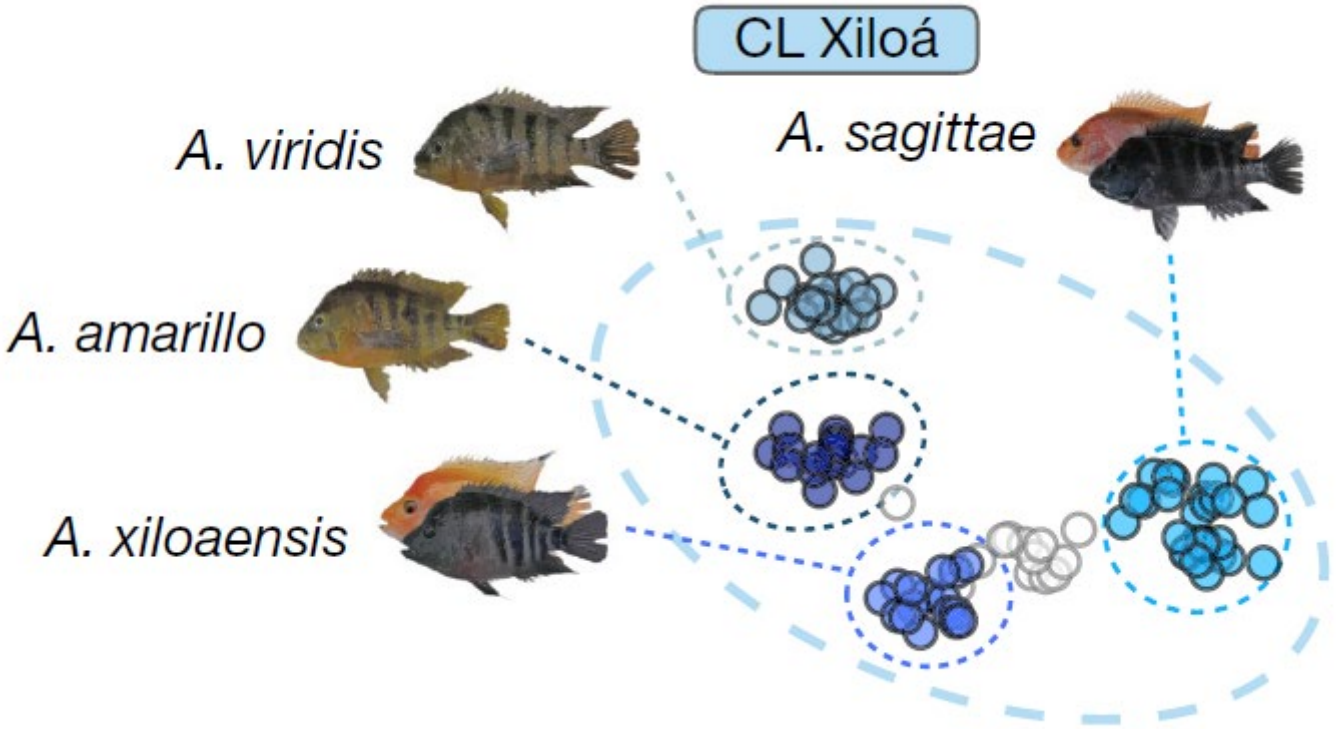
Zefu Wang et al. 2021

Nicaraguan crater lake *Ampophilus* cichlids:

many sympatric species thought to have diverged in sympatry

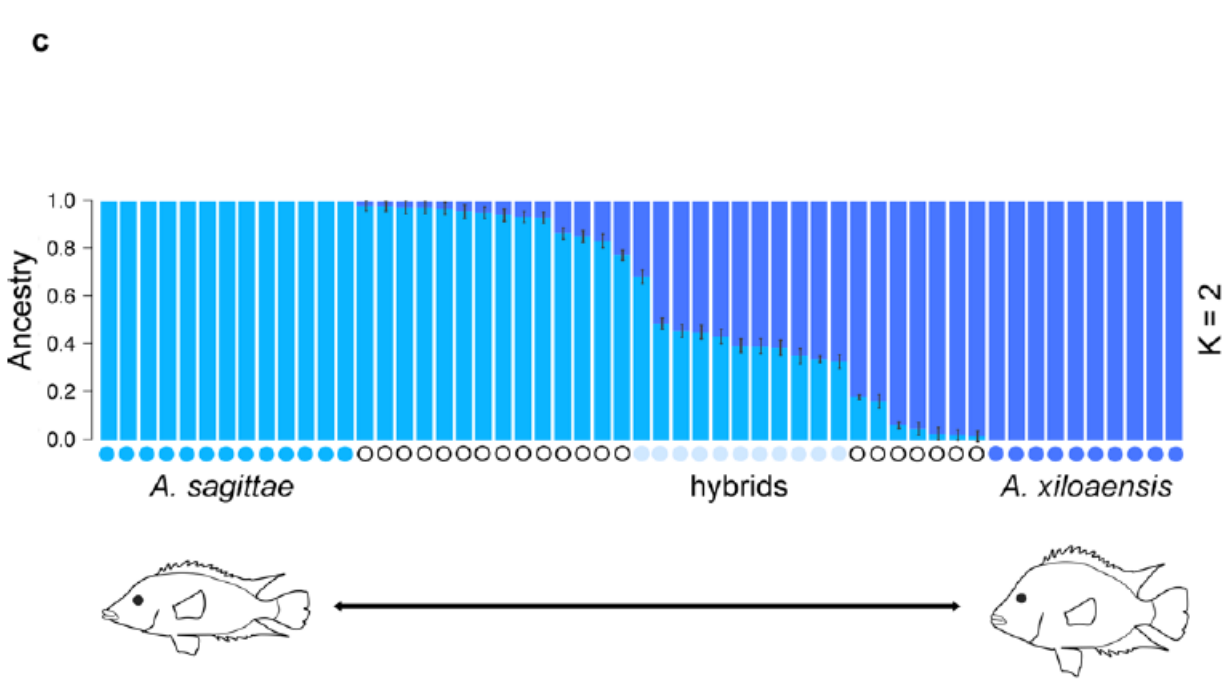


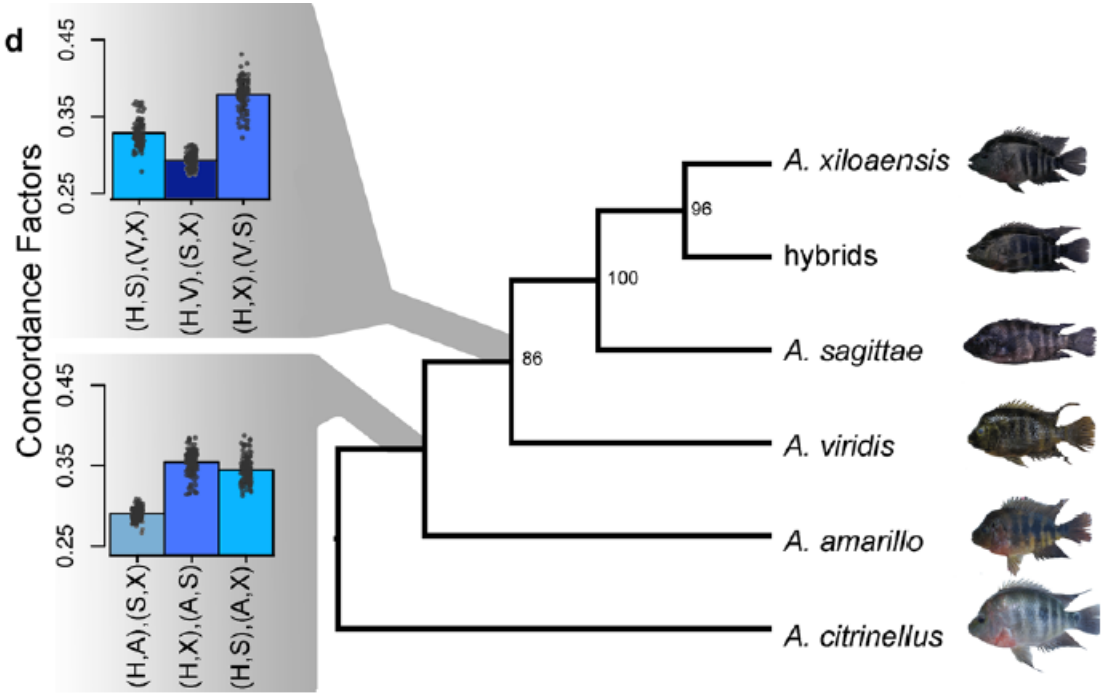
Amphilophilus sagittae x *A. xiloaensis*: young hybrid species?



Kautt et al. 2020

Amphilophilus sagittae x *A. xiloaensis*: young hybrid species?



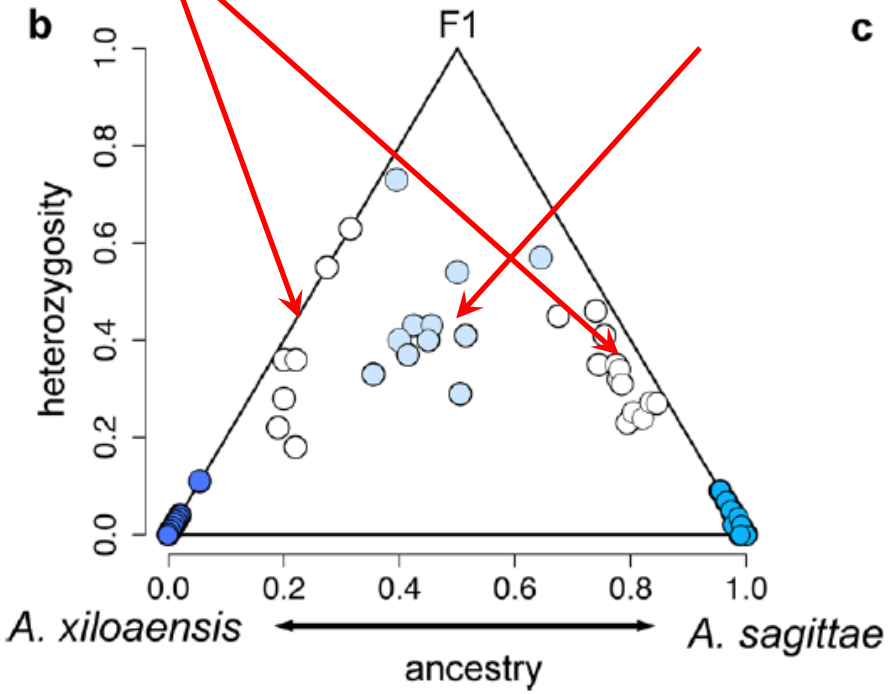


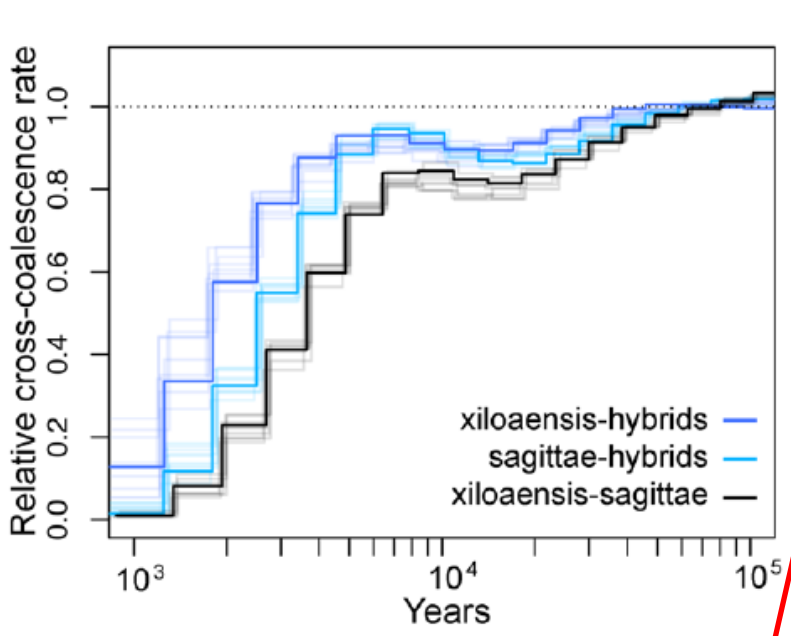
Olave et al. 2022

Amphilophilus sagittae x *A. xiloaensis*: young hybrid species?

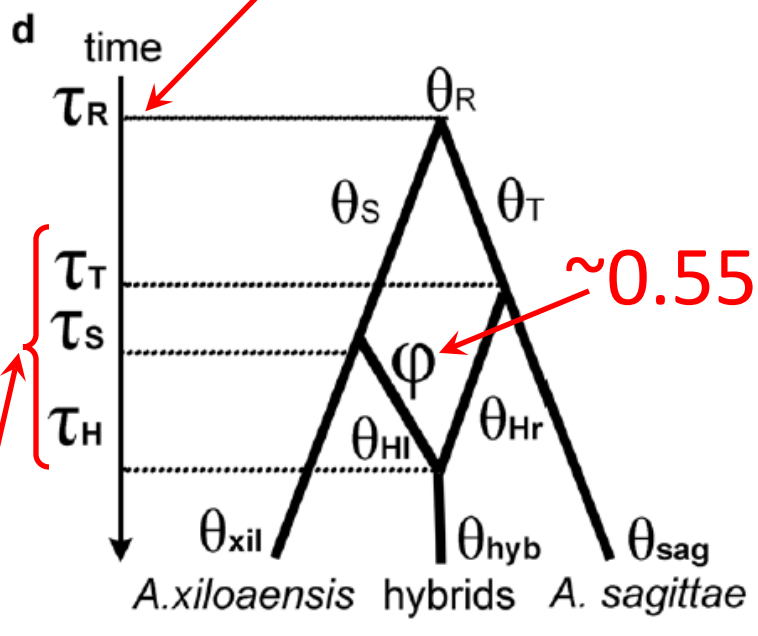
backcrosses

"hybrids"





~2500 generations



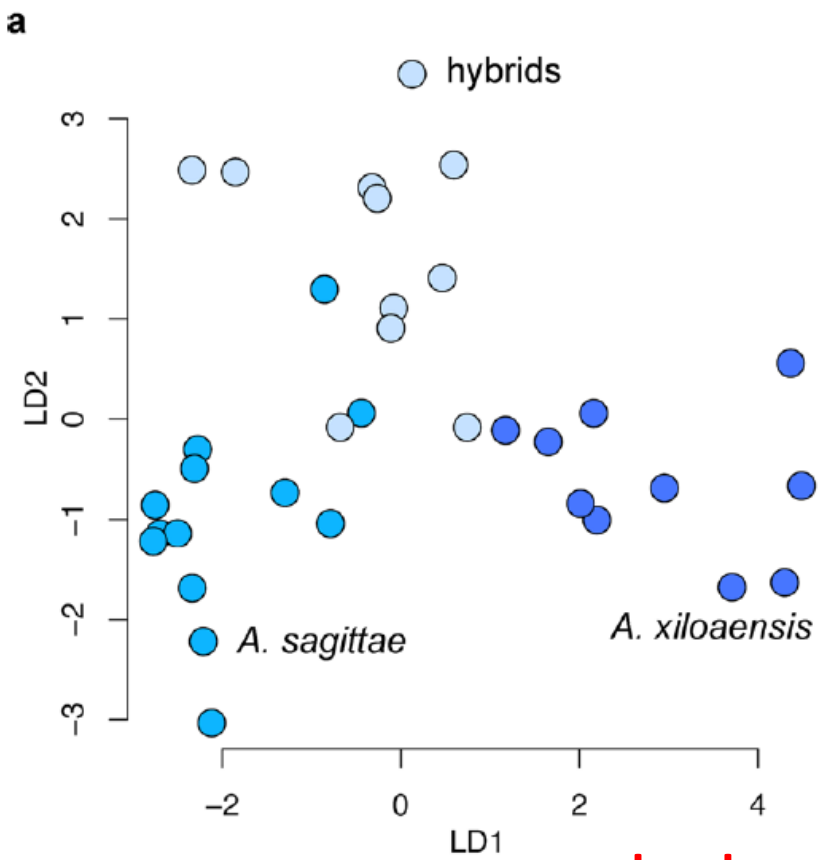
~250 generations

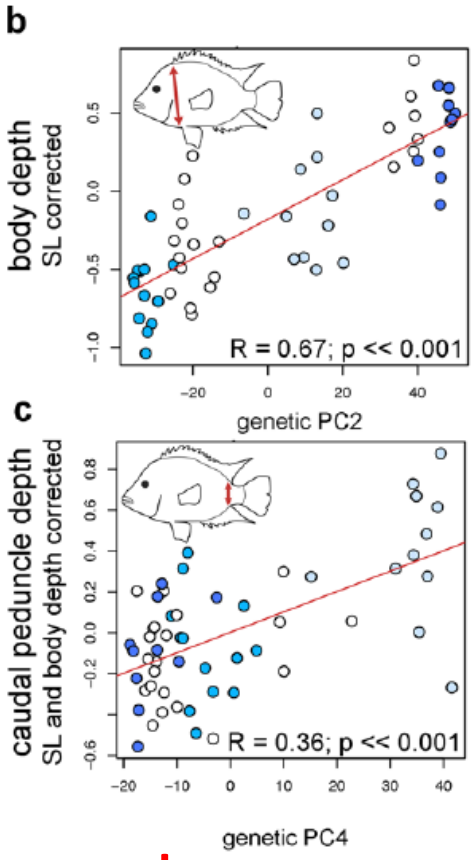
Olave et al. 2022

Amphilophilus sagittae x *A. xiloaensis*: switch in diet?

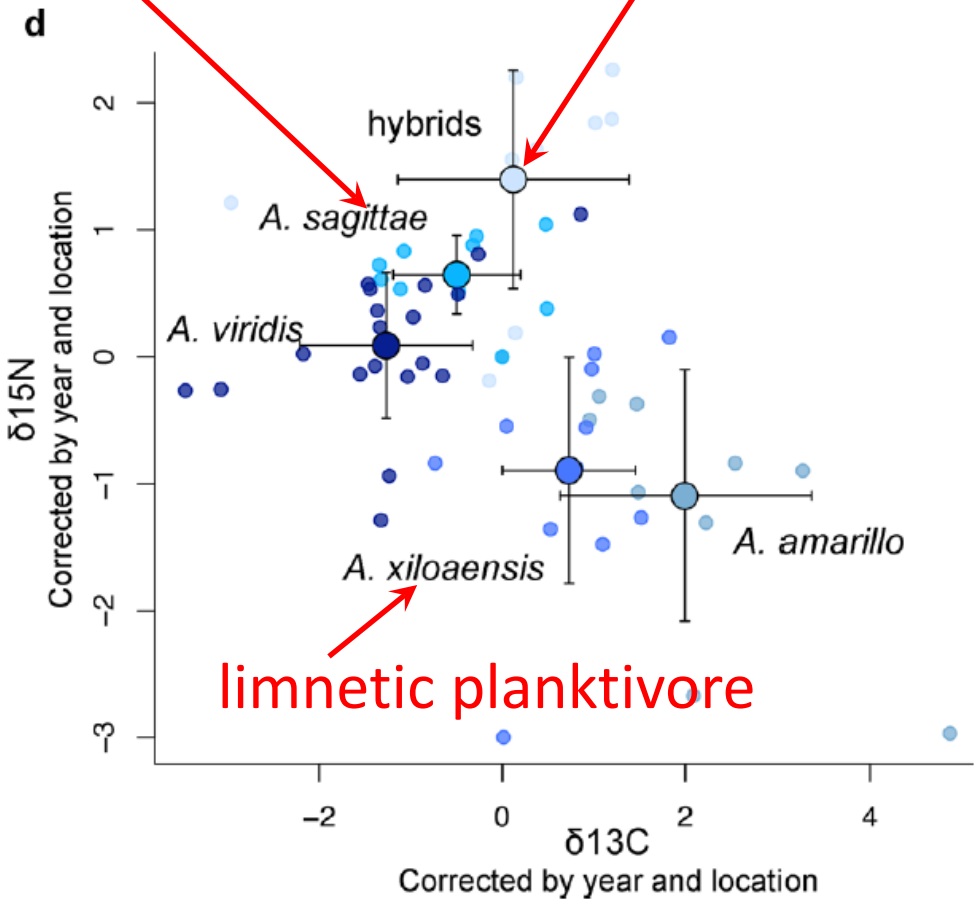
benthic, ?molluscivore

more piscivorous?





morphology analyses

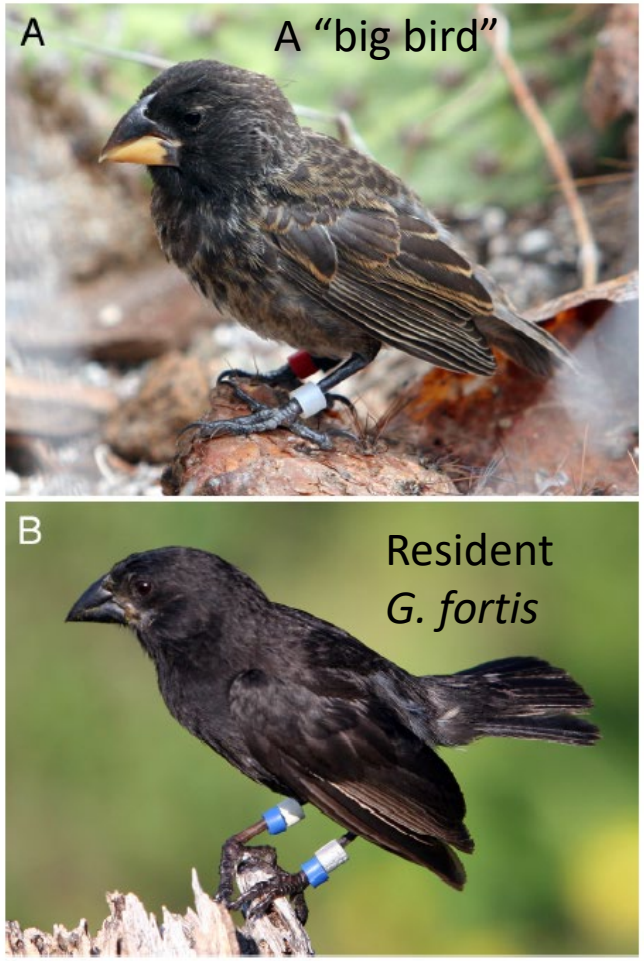


limnetic planktivore

isotope data

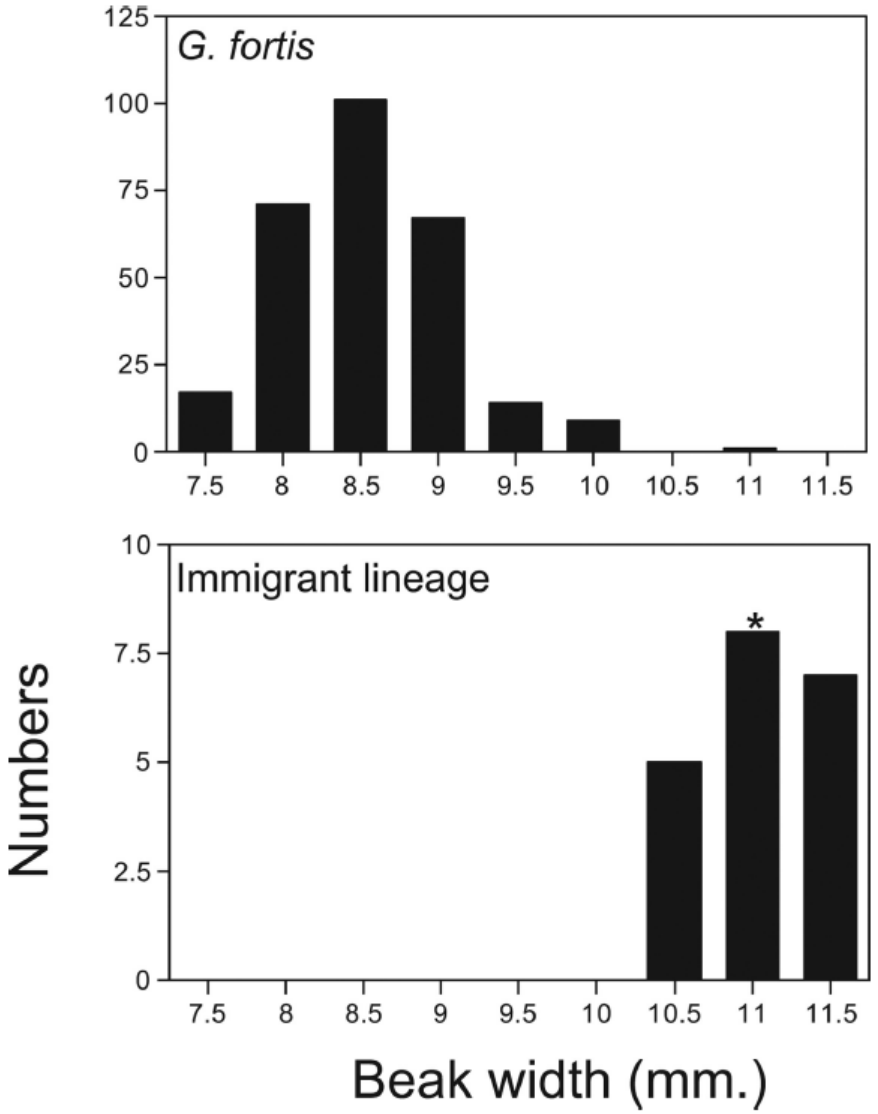
Hybrid speciation in Darwin's finches: "Big Bird"

- An unknown immature male finch immigrated to Daphne Major (0.34 km^2) in 1981. "It resembled local *Geospiza fortis*, but was 70% larger and sang a distinctive song"
- Bred with a *G. fortis* female
- One male offspring bred with another G. fortis female. Two other offspring did a sib-mating
- One offspring of each mating mated with each other producing two offspring that again sib-mated.
- Their offspring produced at least 4 more generations of offspring, the "big bird" lineage. All further matings were with other big-birds.
- A new hybrid species, that sings a distinctive song!



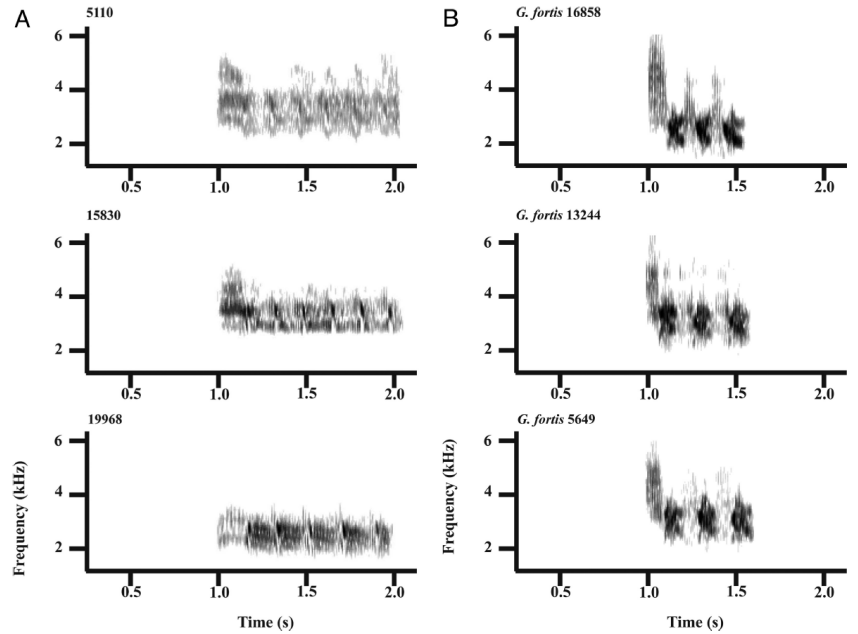
Grant & Grant 2009

Hybrid speciation in Darwin's finches: "Big Bird"



"Big bird" song

Resident *G. fortis*



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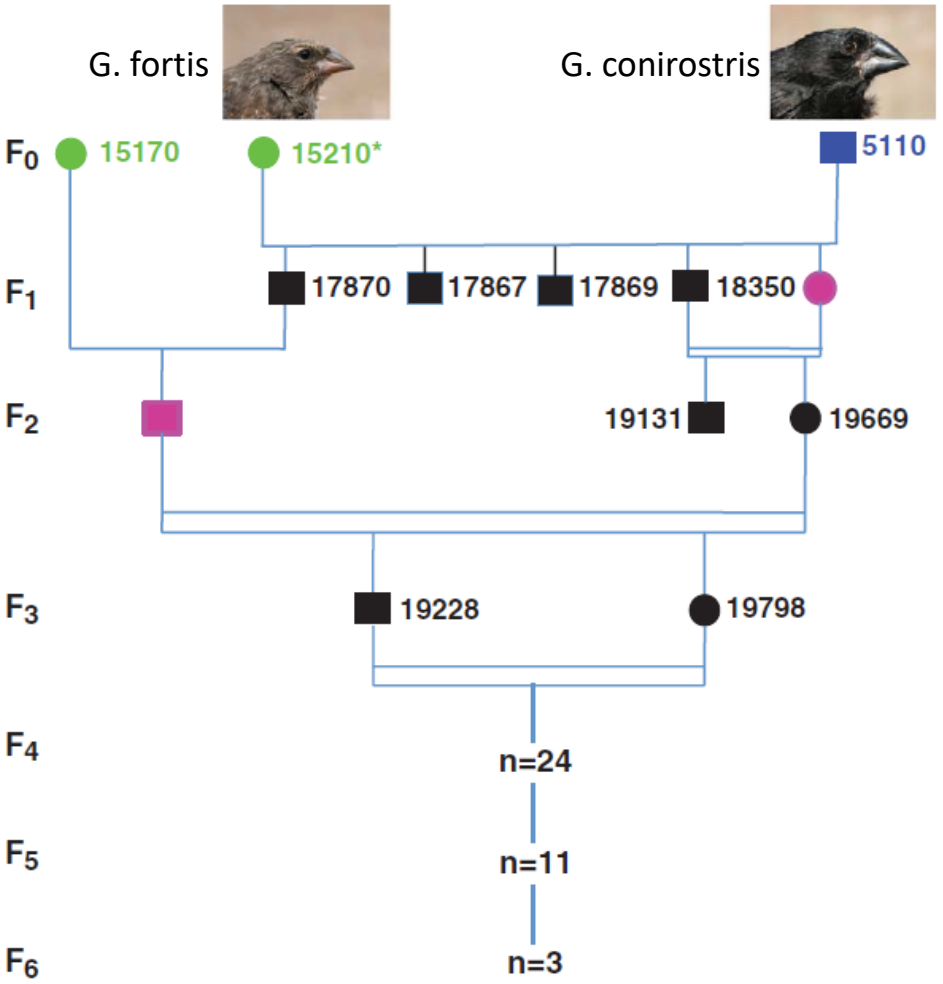
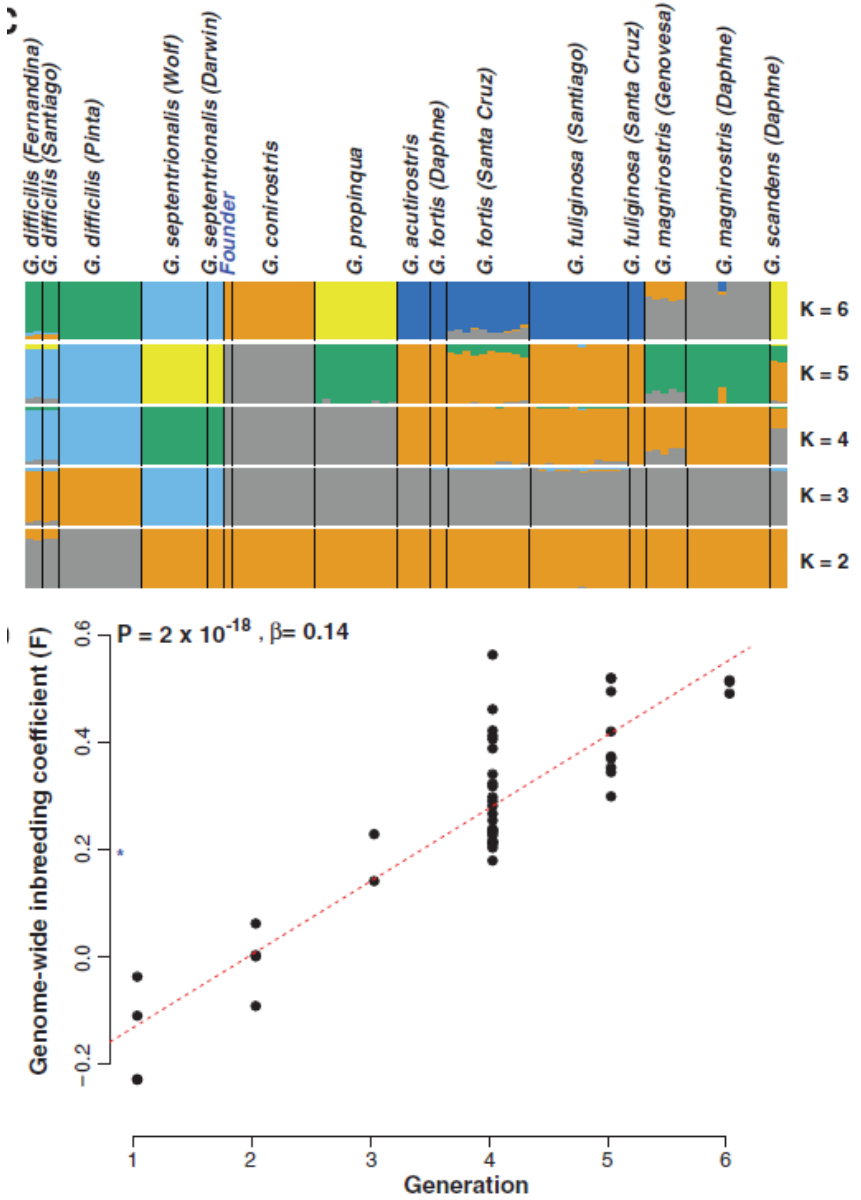
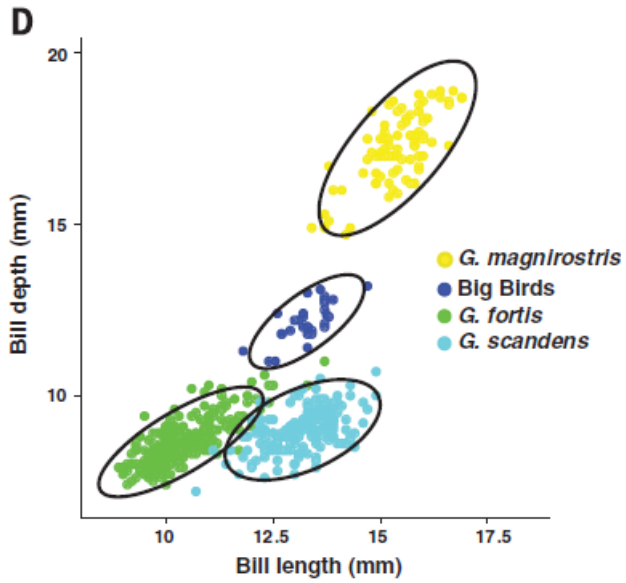
Hybrid speciation in Darwin's finches: "Big Bird"





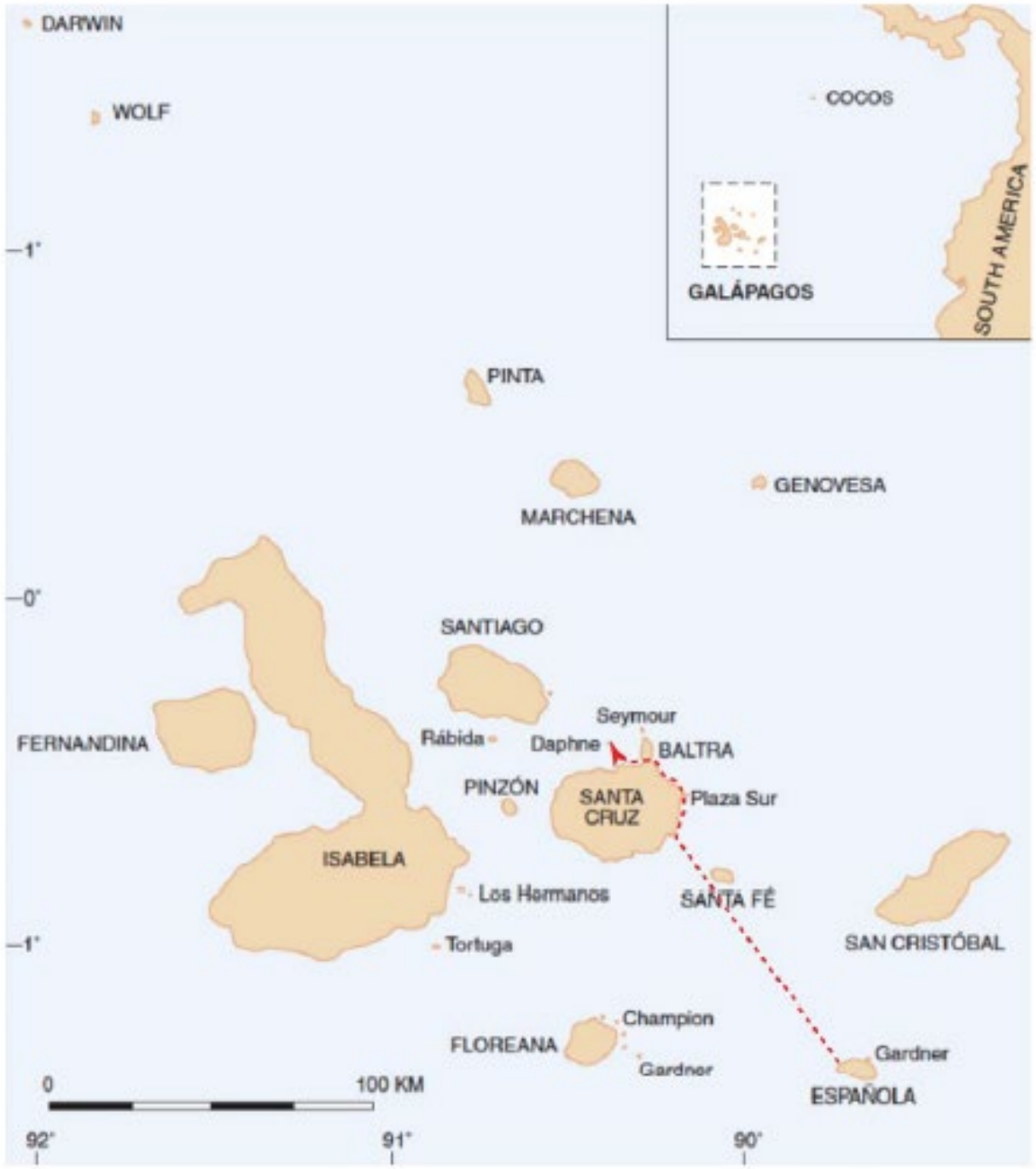


Lamichhaney et al. 2018

Big Bird's male ancestor travelled far!

Would be interesting to know what *G. conirostris* from Española's song is like

Also whether "big bird" is as isolated from *G. conirostris* as it is from *G. fortis*



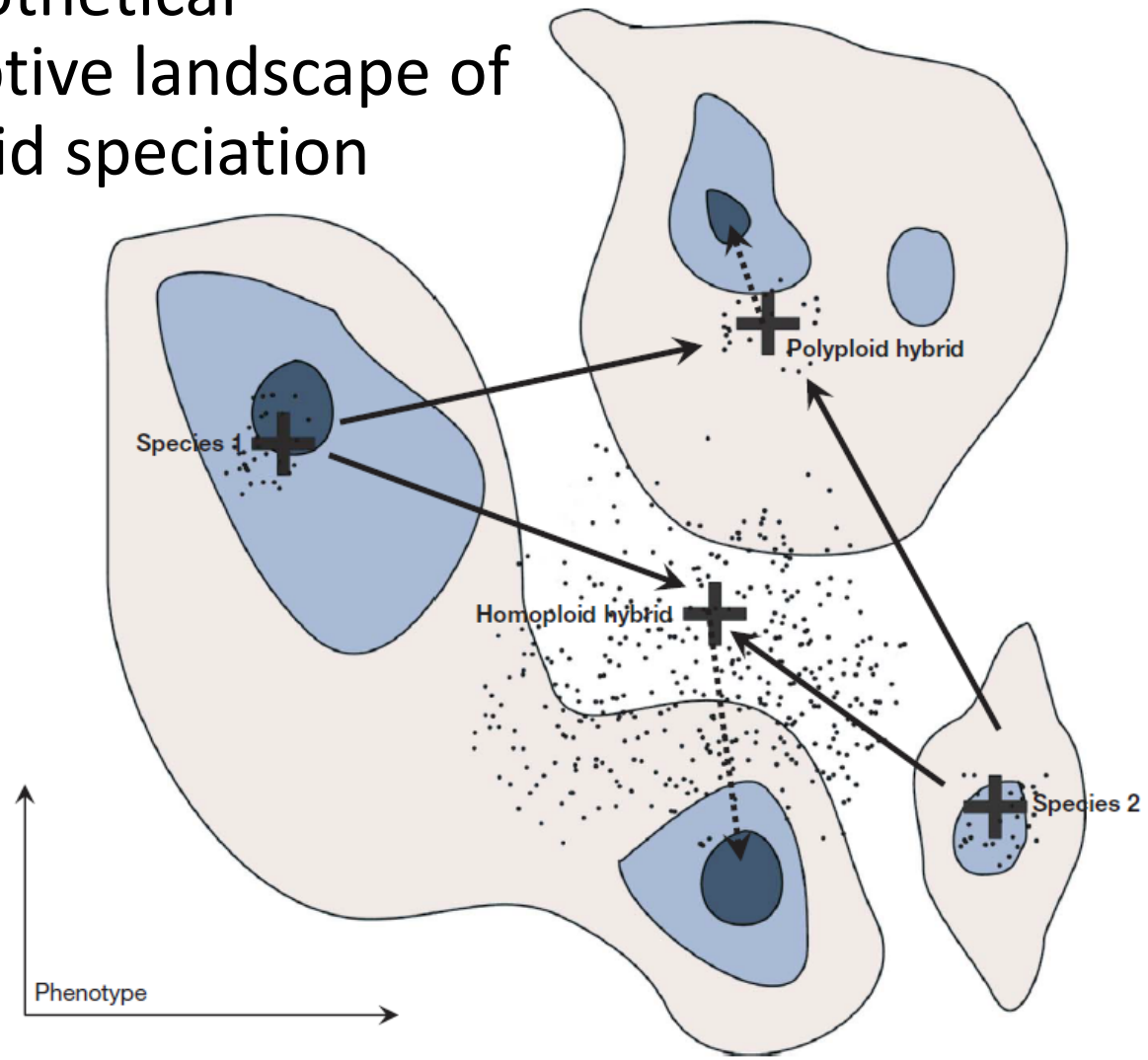
Hybrid speciation seems unlikely

A new hybrid seems like a “hopeful monster” (Goldschmidt’s term)!

Also, if species are reproductively isolated, how could a hybrid become reproductively isolated from both parents?

Homoploid hybrid species: “transgressive variation” in quantitative traits: + + + – – and – – – + + genotypes can hybridize to produce – – – – – and + + + + + transgressive variants

Hypothetical adaptive landscape of hybrid speciation



Hybrid speciation: seems unlikely, but it happens!

- Hybrid species are like “hopeful monsters”!
- Yet alloploid hybrid speciation very common, maybe >10% of speciation events in plants. Many useful crops are allopolyploid. In fungi, allopolyploidy led to bakers’/brewers’ yeasts.
- In animals, chromosome doubling is rare. But has occurred. Allopolyploidy? We don’t know.
- Homoploid hybrid speciation. Seems unlikely, but these studies show it does happen. How common? We don’t know, but we see introgression a lot, and also early stages of hybrid speciation in nature. These facts suggest it could be very common.
- Partly depends on definitions of what we mean by species, and what we mean by homoploid hybrid species (as opposed to merely introgressed lineages). Perhaps we shouldn’t be too strict?