Sympatric speciation

Today:

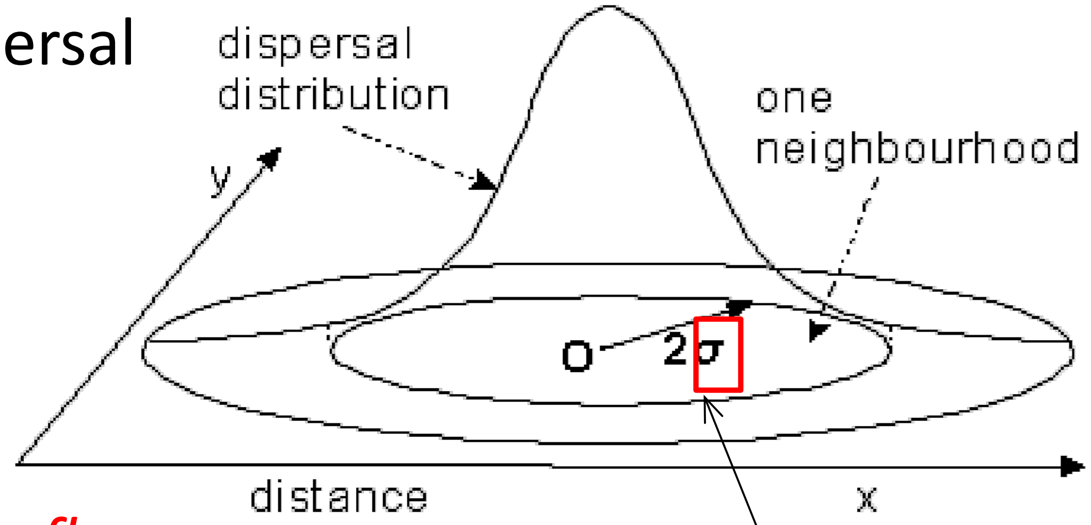
Is speciation possible in sympatry?

Viewed as more difficult, because divergence must take place in the presence of homogenizing gene flow.

Why does geography matter?

Because *dispersal* *is limited!* Dispersal and gene flow is often misunderstood, even by some evolutionists

Population geneticists often call dispersal *migration*, but do not mean the kind where birds return after migration to near their parents nest!

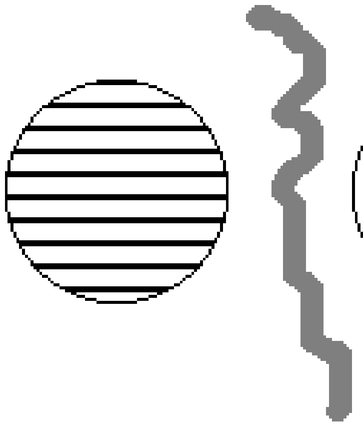


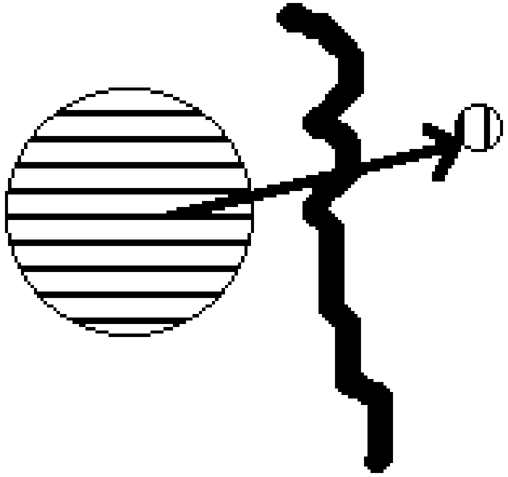
Dispersal by individuals leads to *gene flow* (though we usually mean *genotype flow*)

Gene flow can prevent divergence due to selection, drift

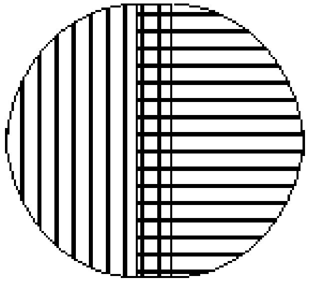
Geographic definitions

Allopatry

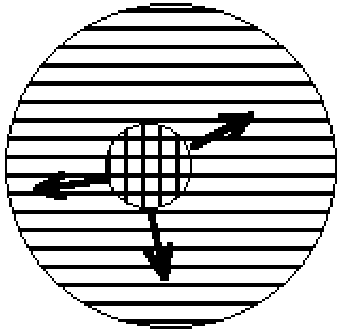




Parapatry



Sympatry. Speciation is sympatric if it occurs within individuals' "cruising range"



Geographic definitions

Sympatry: '... if individuals of each are physically capable of encountering one another with moderately high frequency. Populations may be sympatric if they are ecologically segregated, as long as a fairly high proportion of each population encounters the other along ecotones; and they may be sympatric, yet breed at different seasons'

Parapatry: ... groups of populations occupying 'separate but adjoining regions, such that only a small fraction of individuals in each encounters the other'

Allopatry: '... separated by uninhabited space (even if it is only a very short distance) across which migration (movement) occurs at very low frequency'

'The conditions under which host-associated sympatric speciation might occur are so exacting as to be met by very few species.'

Futuyma & Mayer 1980

What is sympatric speciation? What is sympatry?

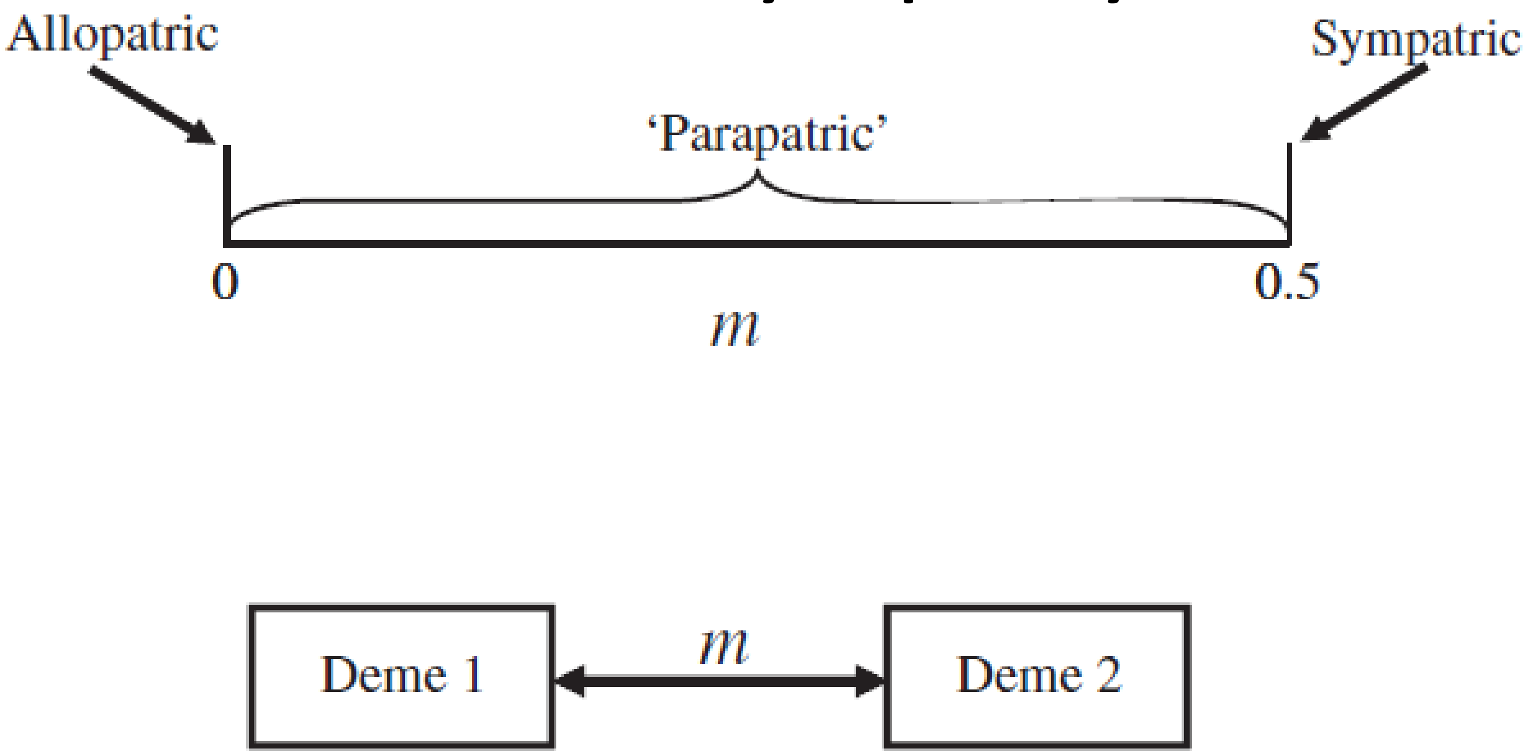
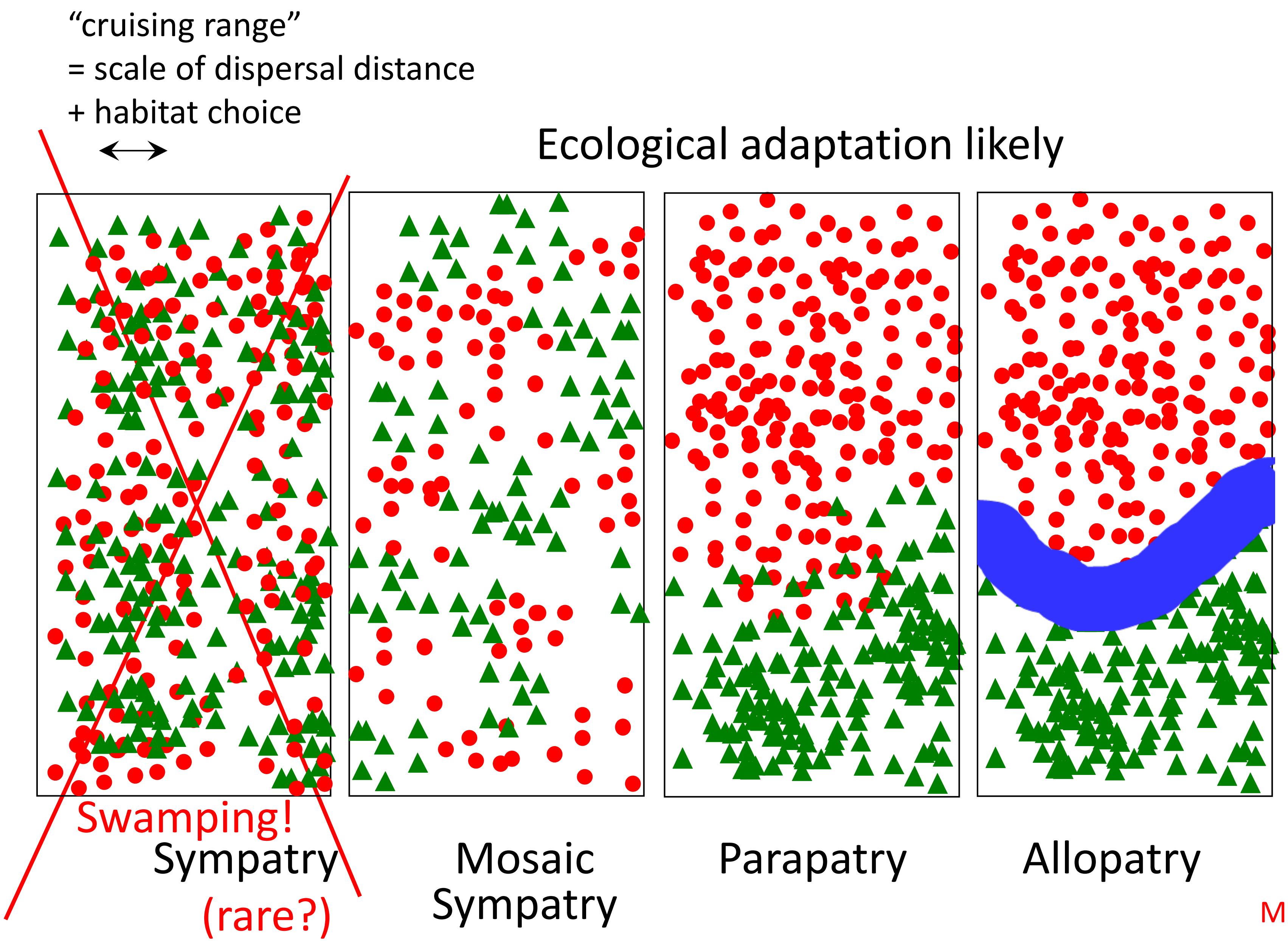


Fig. 1 Demic view of sympatry and allopatry in the Gavrilets (2003) formulation.

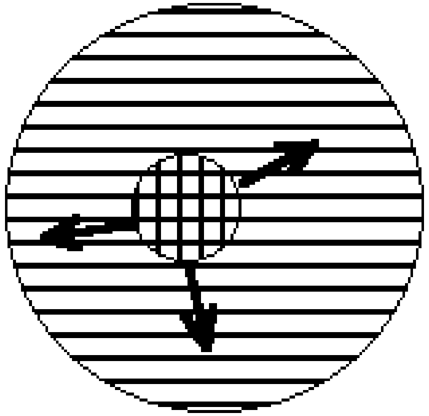
Gavrilets 2003; Mallet et al. 2009

Rethink of sympatry vs. parapatry



Mallet et al. 2009

Sympatric speciation



Classical view:
Like parapatric speciation, sympatric speciation requires (a) divergent selection or (b) polyploidy to generate "post-mating isolation," and ... (c) reinforcement and/or pleiotropic changes in mate choice (to generate "pre-mating isolation").

Selection must occur under high levels of gene flow within the normal "cruising range", so selection must be very strong ⇒ considered rather unlikely by Ernst Mayr (1963) and Coyne & Orr (2004)

However, sympatric speciation would potentially be very rapid, so could be important? (e.g. speciation due to polyploidy ≈ 3%-15% of total speciation in flowering plants and ferns).

Coyne & Orr (2004) criteria

p. 142: "… we will consider allopatric speciation as the null hypothesis when evaluating examples in nature. That is, we will deem allopatric speciation as the most likely explanation unless sympatric speciation appears more plausible." Why?

- Allopatric speciation is "easier": divergence can occur with little (or no) selection
- Much evidence for allopatric speciation; little for sympatric speciation
- Geographic isolation is common & likely (e.g. glaciations etc.).

… a/c Coyne & Orr 2004

Criteria for sympatric speciation:

1. Species must be currently largely, or completely sympatric
   (e.g. small island pairs of species)
2. Species must have substantial reproductive isolation
3. Sympatric taxa must be sister species; "this must not result from hybridization"
4. Biogeographic and evolutionary history makes an allopatric phase very unlikely

Sympatric speciation in symbiotic bacteria

- Cicadas feed on xylem sap – very nutrient poor
- They need 10 essential amino acids out of 20
- Around the guts of cicadas and other sucking bugs are special organs called "bacteriomes"
- These house endosymbiotic bacteria that provide vitamins and essential amino acids to the host
- In cicadas, *Sulcia* bacteria provide 8 of 10 essential amino acids, and *Hodgkinia* the other two

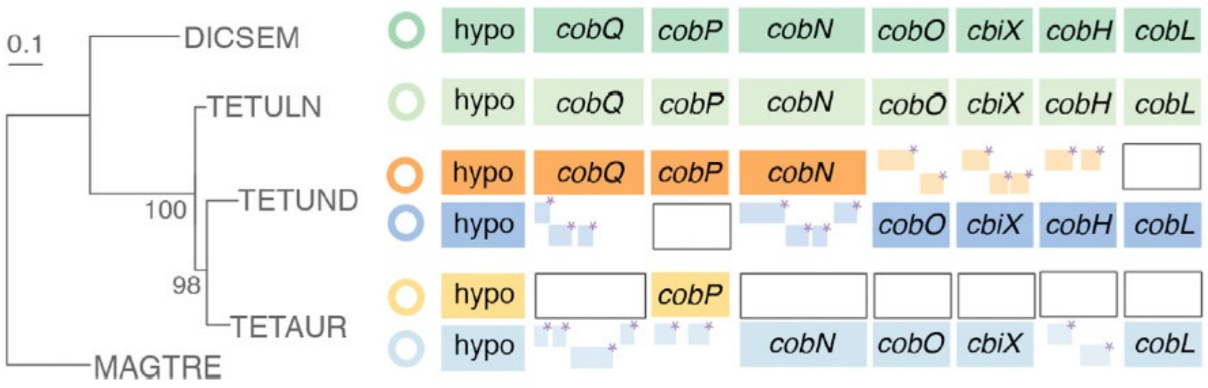
- However, in the cicada *Tettigades undata*, two different *Hodgkinia* were found in bacteriomes

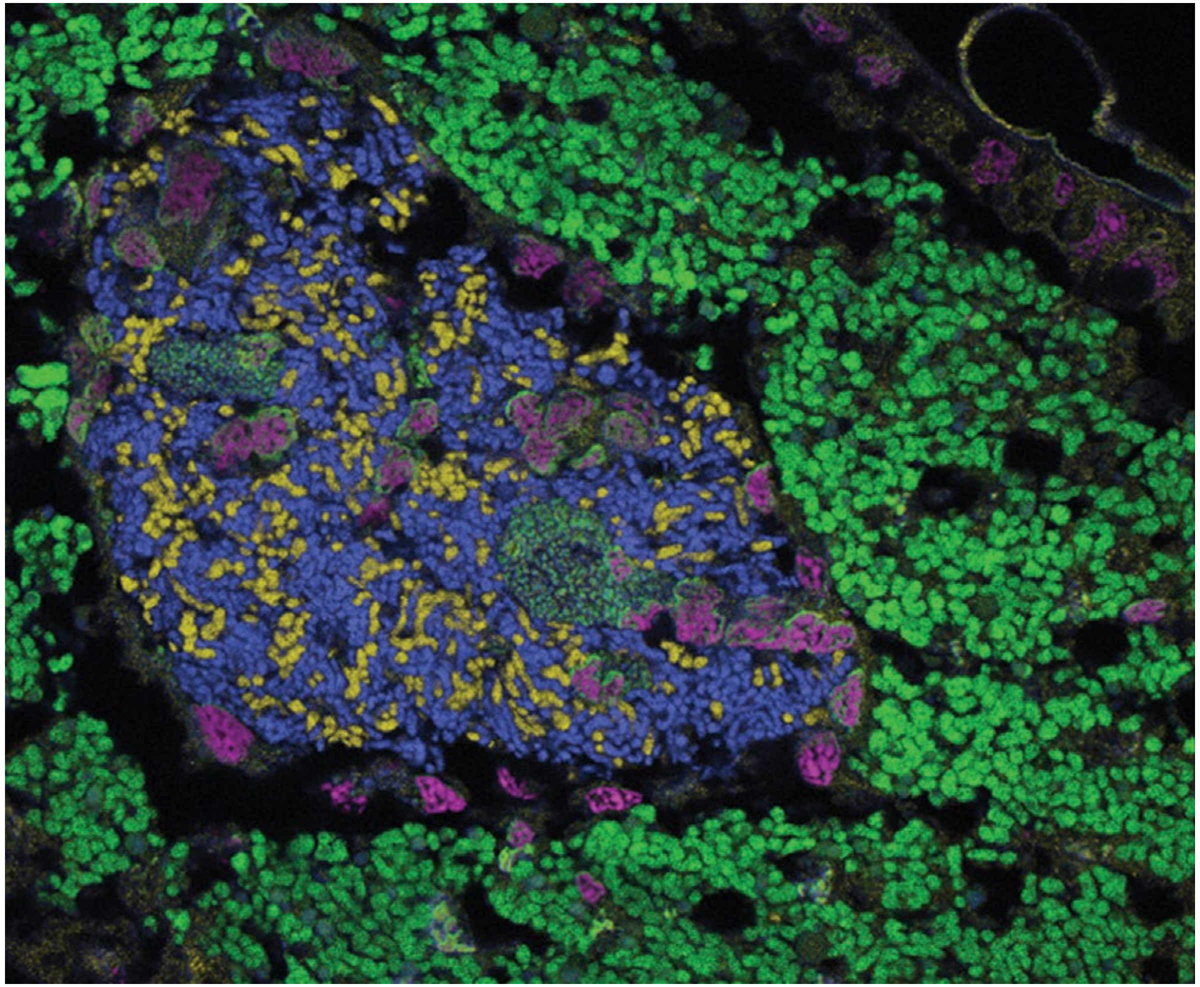
- They appear to have close relationships, but each bacterial species has lost certain key genes, especially in the vitamin B12 pathway

Van Leuven et al. 2014

Hodgkinia species in *Tettigades undata* bacteriome

- Gene loss is common in endosymbionts (think of mitochondria, which originally were bacterial endosymbionts
- But here, gene loss is different in each bacterial species, with one species making up for the losses of the other!





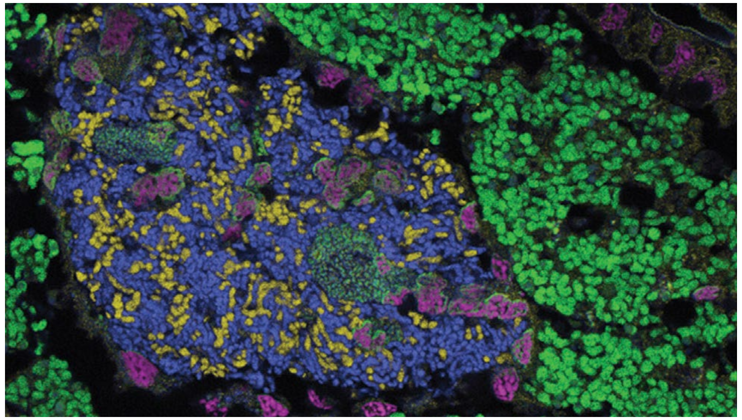
Hodgkinia TETUND1 = yellow
Hodgkinia TETUND2 = blue
Sulcia = green

Van Leuven et al. 2014

Speciation on tiny, remote islands

Examples of “islands”:

- Maternally inherited bacteriome (as in *Hodgkinia* in the cicada)
- Animals and plants on remote oceanic islands
- Fish in crater lakes

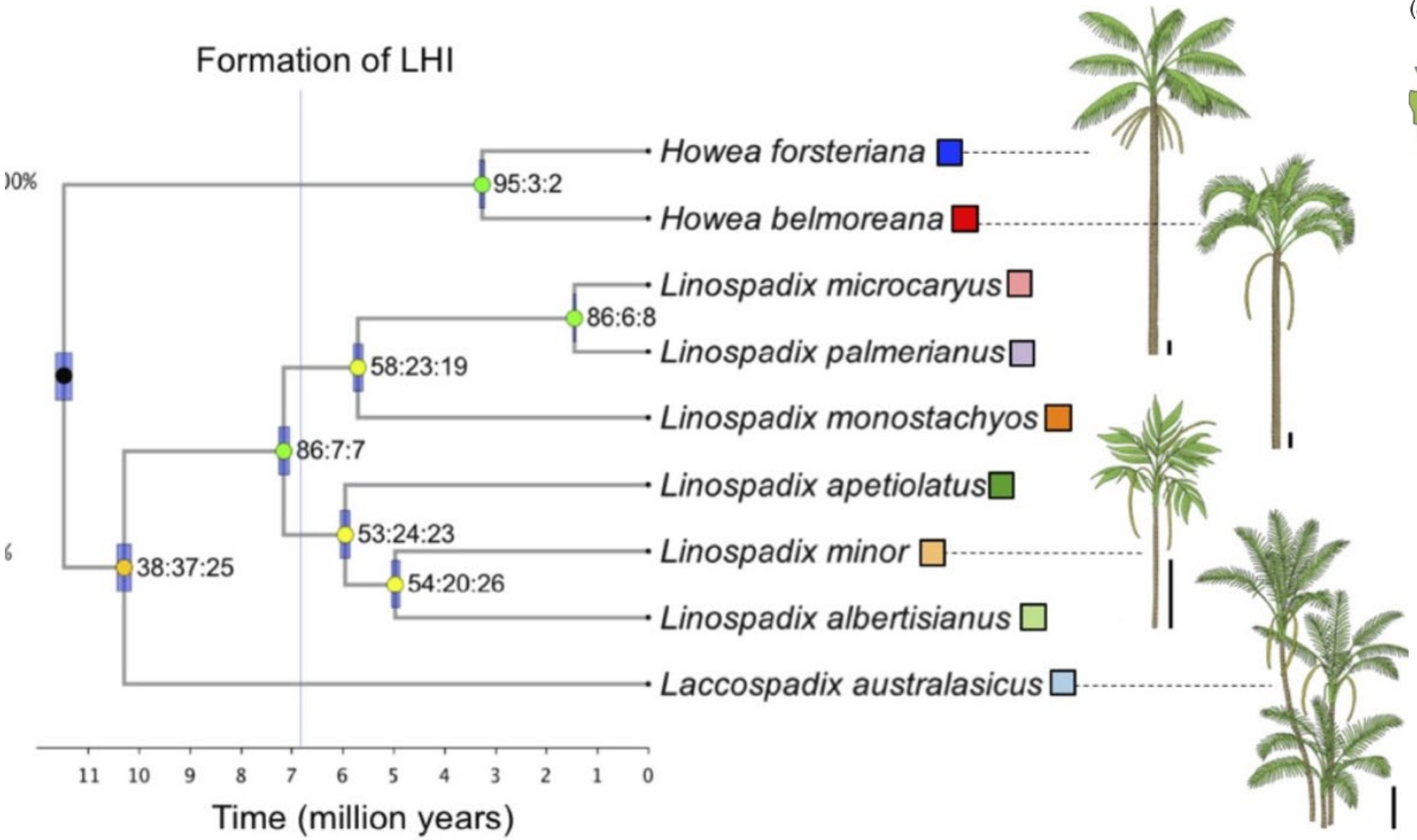


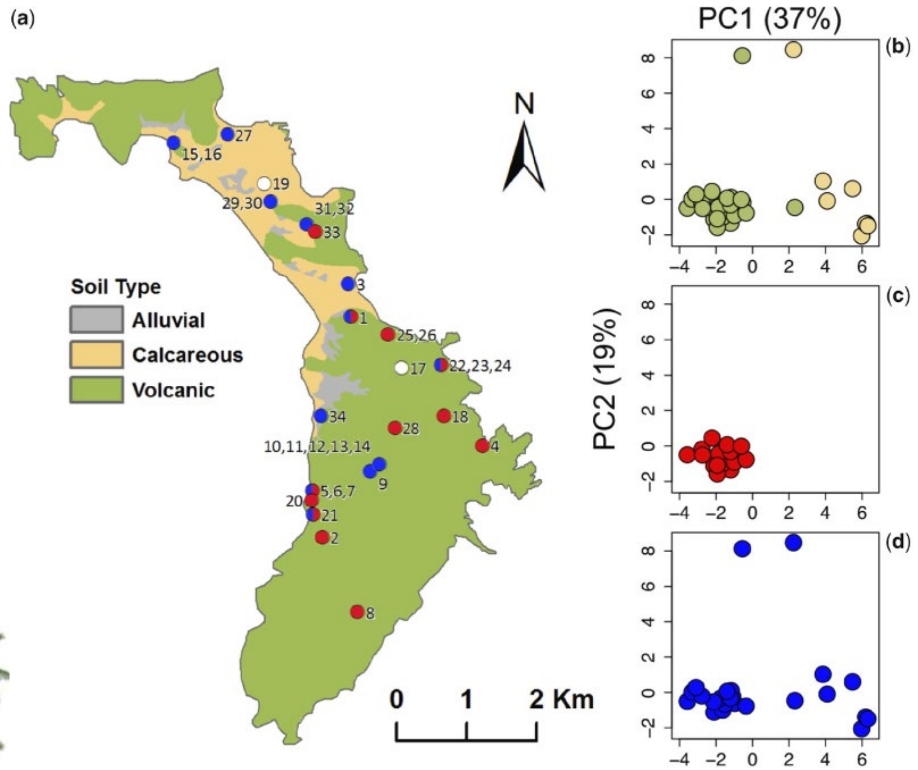
Plant speciation on Lord Howe Island

< 16km^2

~575 km from Australia

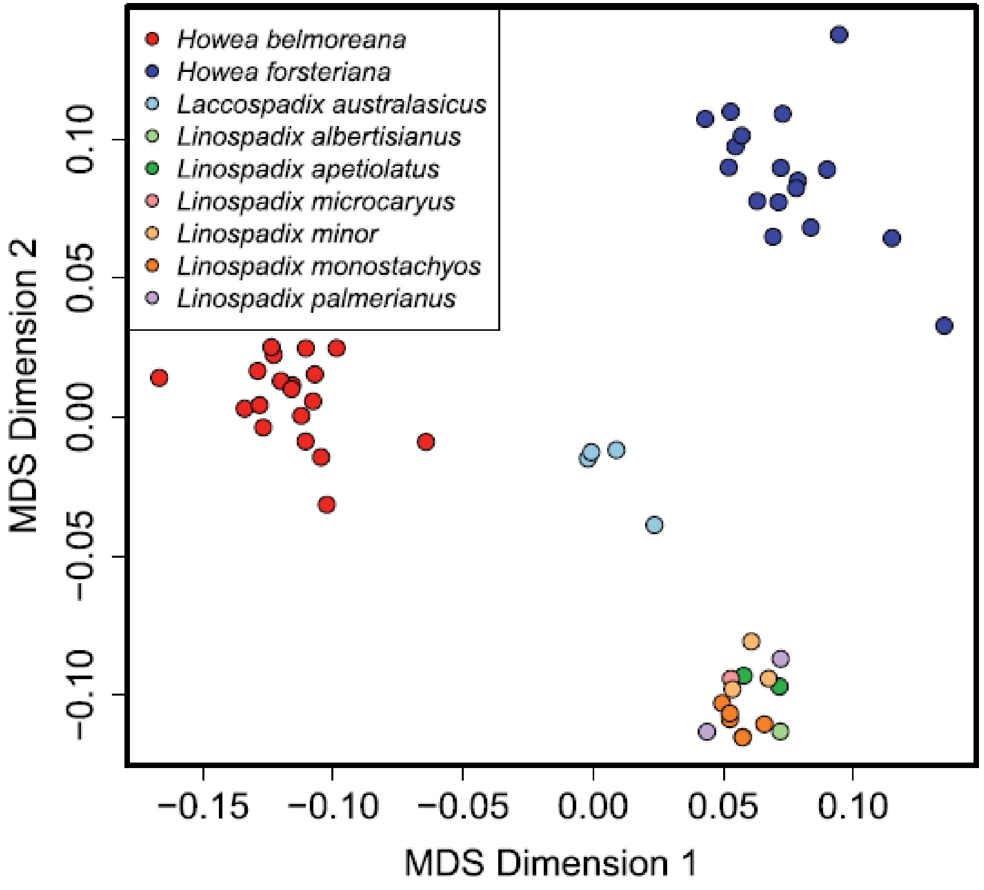
Howea palms
The two species split ~3.3 My ago



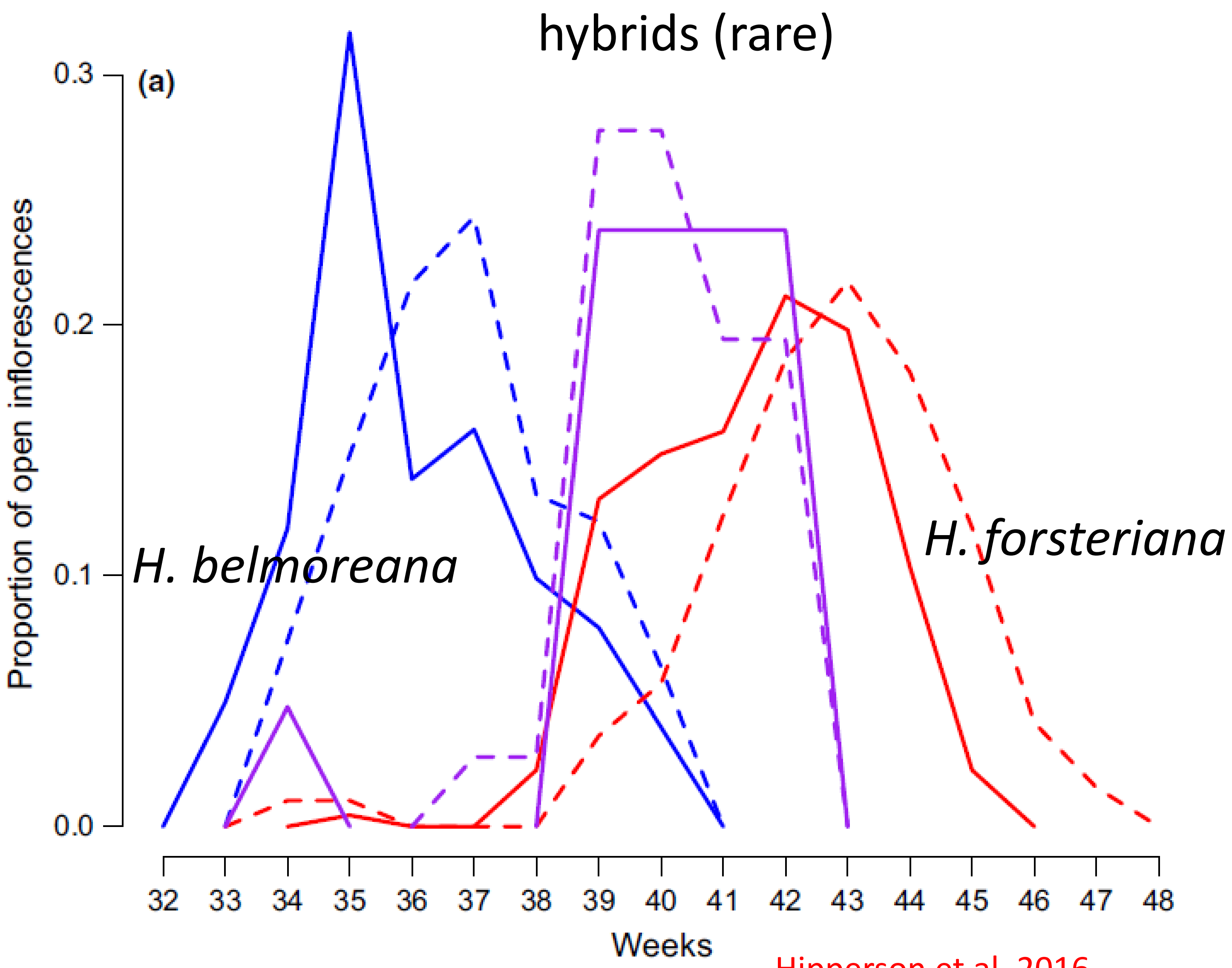


Osborne et al. 2019

Howea palms



Osborne et al. 2019

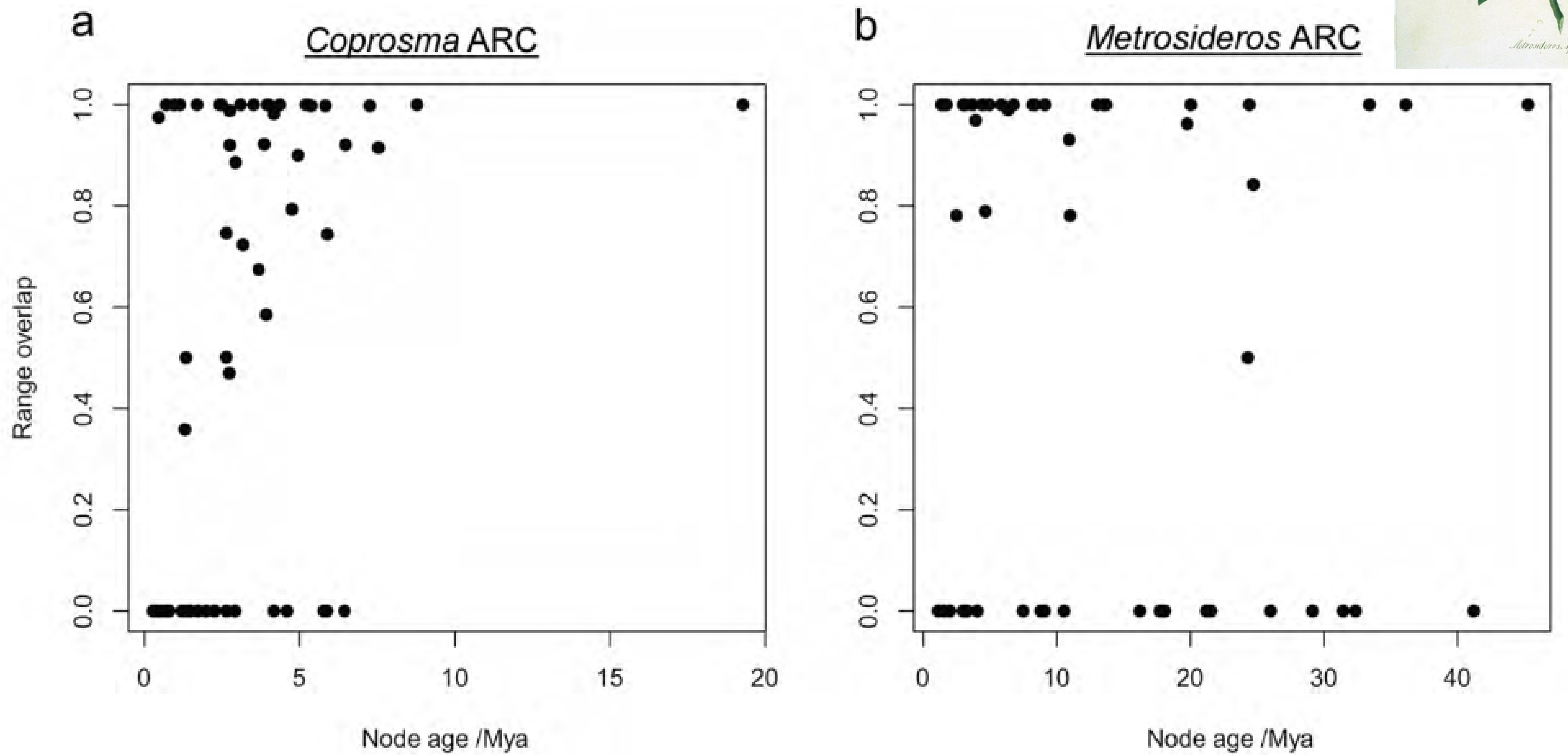


Hipperson et al. 2016

Lord Howe Island

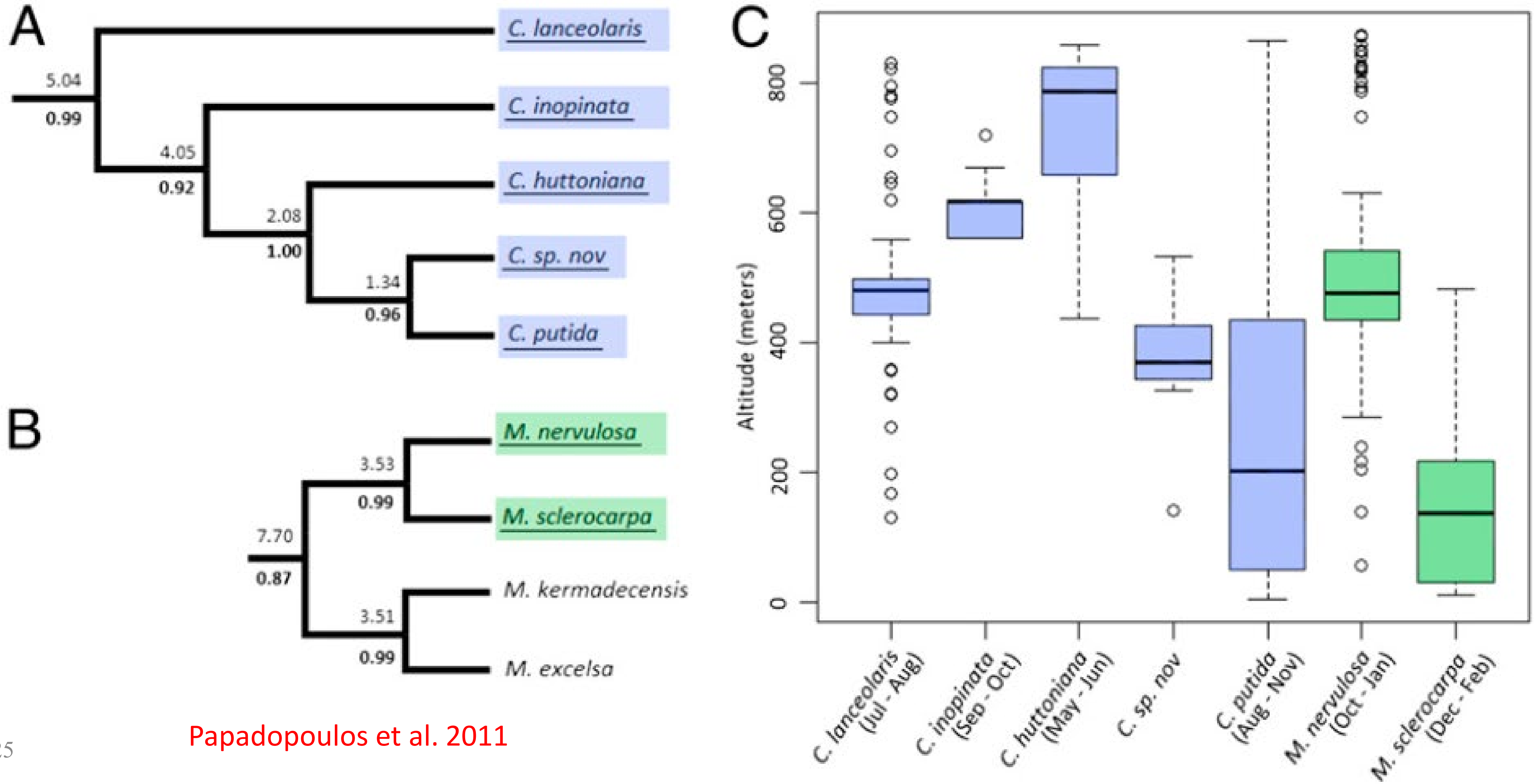
- Tropical, 875 m mountain, many species total: 242 vascular plants
- Many endemic species
- As much as 8% of the flora speciated on Lord Howe Island, i.e. sympatric pairs or divergence after arrival (single endemic species)
- Careful study of 4 genera revealed likely sympatric speciation of four events in *Coprosoma*, and one each in *Metrosideros*, *Howea*, and *Polystichum* (a fern)
- Also, age/range correlations suggest sympatric speciation likely … see next slide

Age-range correlations



Papadopoulos et al. 2011

Coprosma and *Metrosideros* phylogeny, habitat, and flowering time on Lord Howe Island



Papadopoulos et al. 2011

Larch, *Larix decidua* vs. Cembran Pine, *Pinus cembra*

Larch is a deciduous conifer
All new (soft) needles every year

Pine has very tough needles from previous year
Rapid-growing very resinous shoots yearly

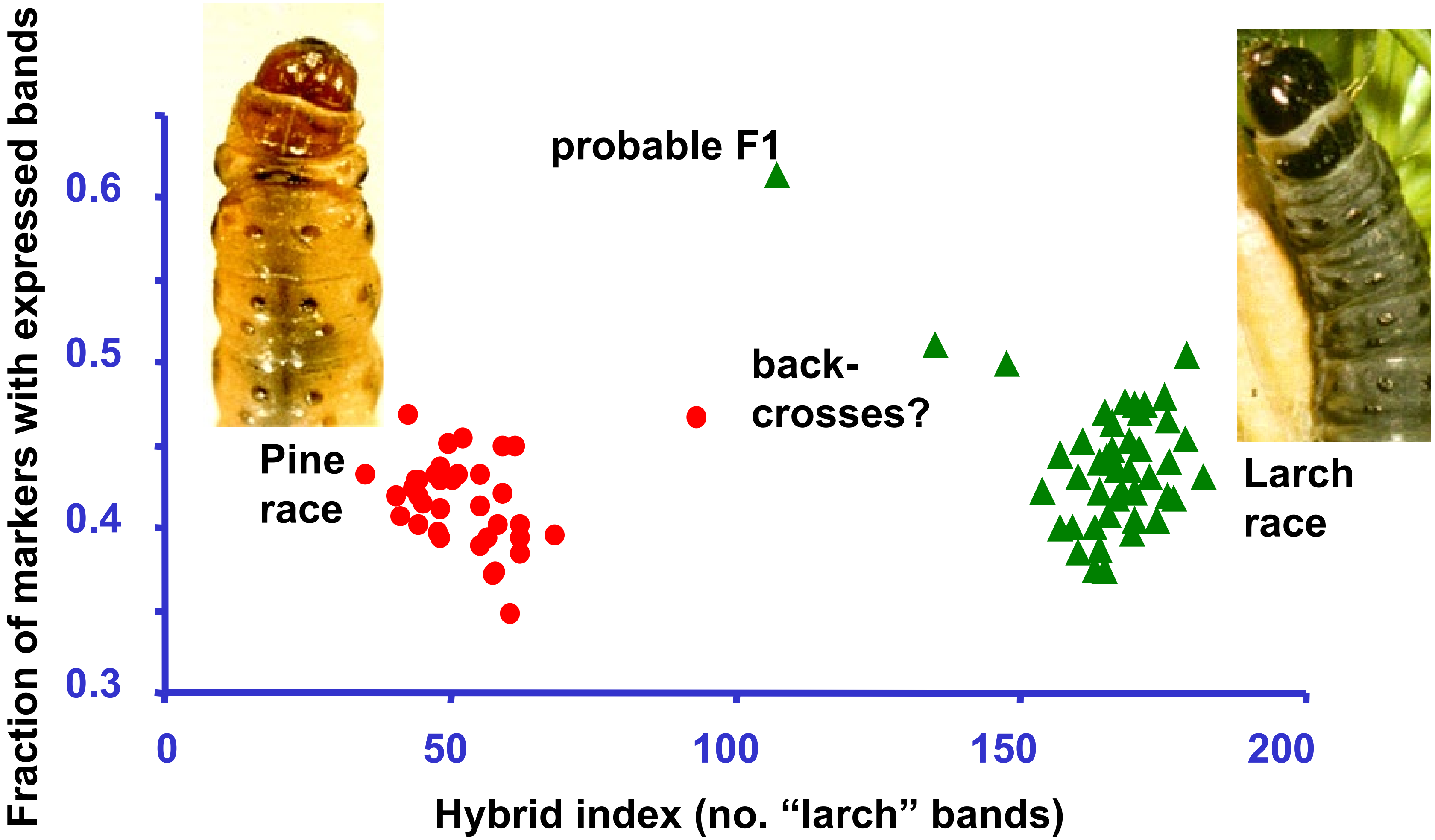
Larch budmoth host races, *Zeiraphera griseana*

Below species:
ecological “races”

Larch

Pine

Genetic differences (AFLP) in *Zeiraphera diniana* (now *Z. griseana*)



Emelianov et al. 2004. Proc Roy Soc B 271: 97–105

Larch budmoth
"host races":

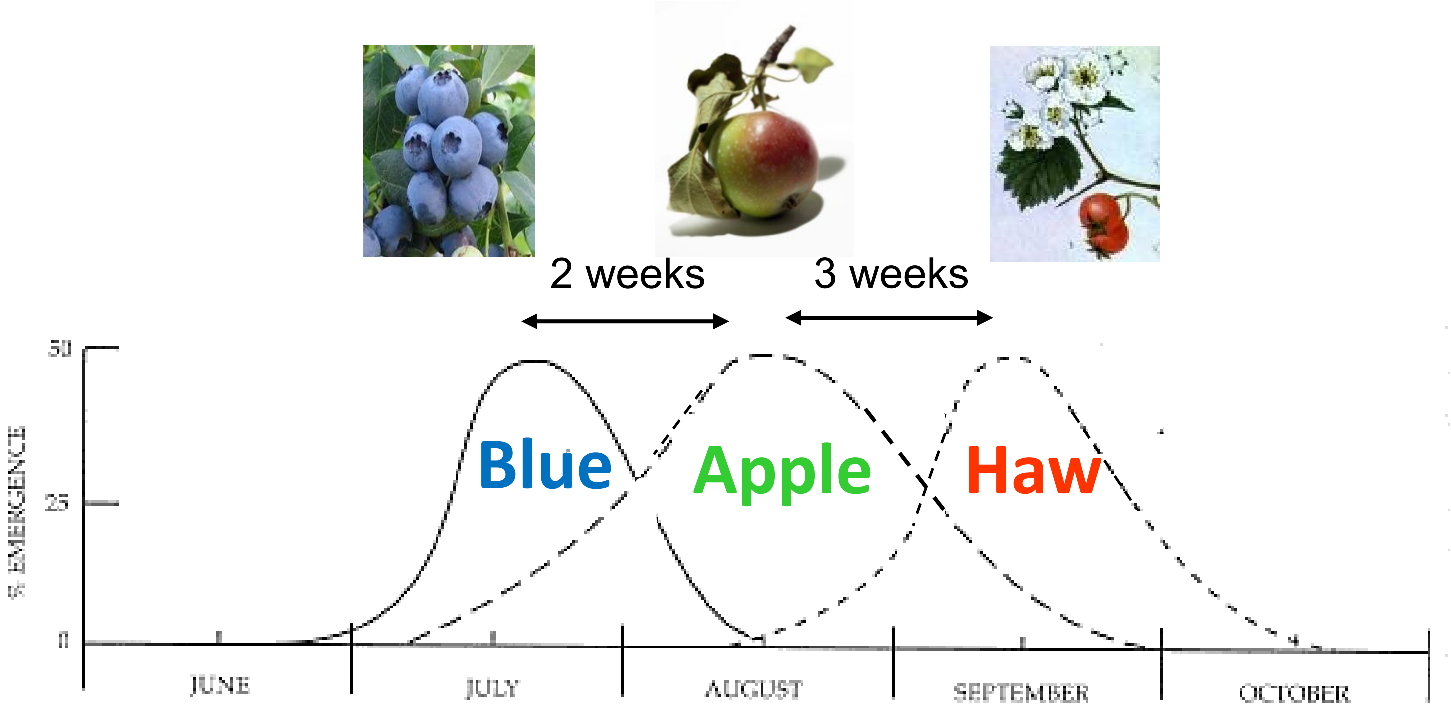
as well as host,
differ in sex
attractant
pheromone

Host "races" in the apple maggot, *Rhagoletis pomonella*

You may remember this:
Native host: *hawthorn*
Became *apple* pest in 1860s, due to a host switch
Apple-eating form quickly spread all over E. USA

1. Females prefer to lay on own host (*host races*). Races differ in frequency of molecular markers (but few "fixed" differences)
2. Races hybridize, m $\approx$ 0.06 per generation
3. Races do not differ in survival (apple always worst host)
4. Parasitoids less successful with apple larvae (*ecological release*)
5. Males use host fruits as mating venue. So host switch has a *pleiotropic effect* on assortative mating. So-called "magic trait."
6. Apple race flies earlier than hawthorn race. *Pleiotropy* again (*allochrony*)

Allochronic (seasonal) ecological isolation



Ripe host fruit for adult mating, female oviposition, and larval feeding are seasonal resource islands that overwinter diapause timing of flies must match to maximize fitness

Flies have one generation per year, live < 1 month, results in pre- and postzygotic RI

Host races in the apple maggot

Little evidence for reinforcement

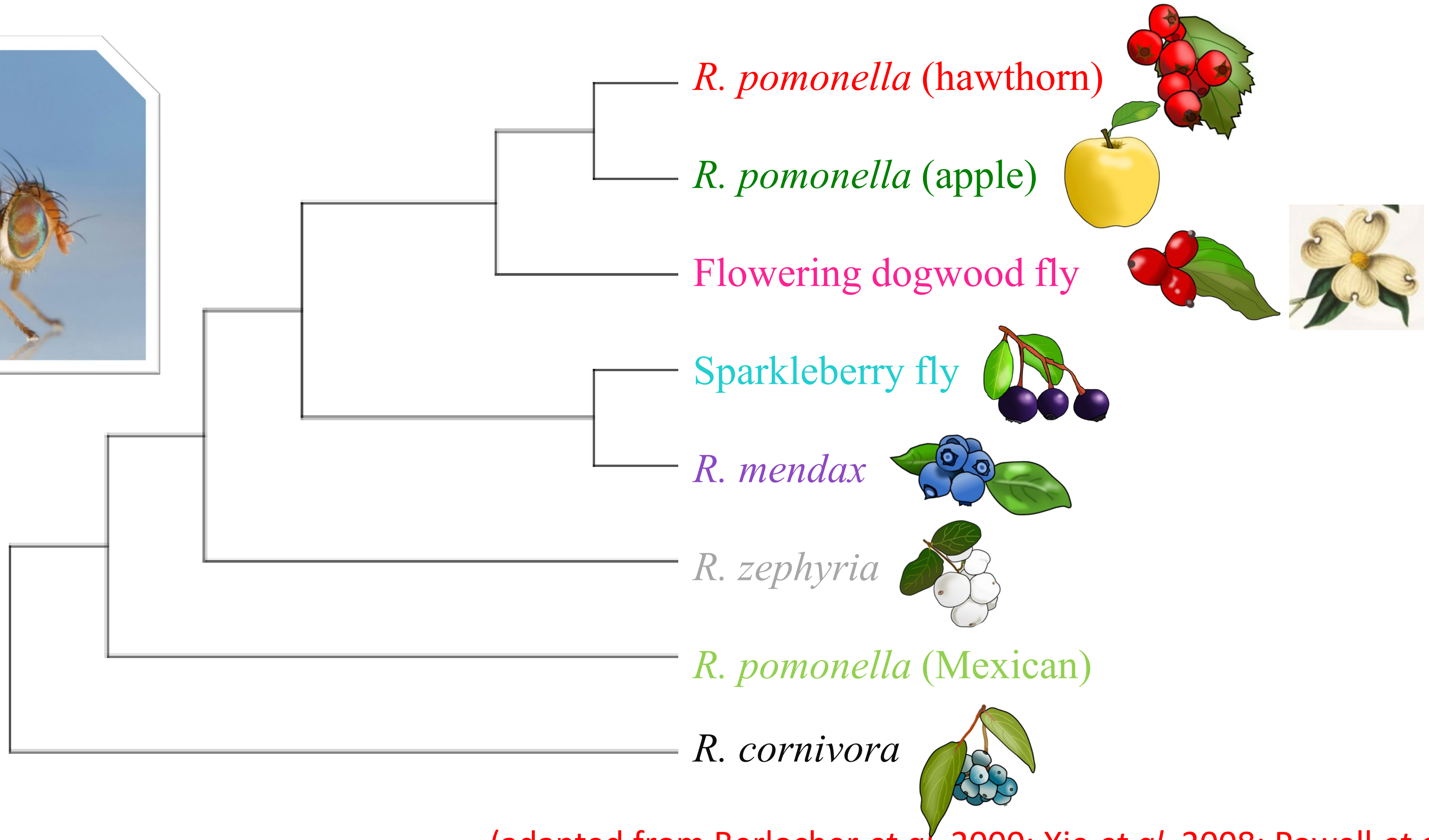
Host choice is a “magic trait” – a pleiotropic adaptation to host plant leads to assortative mating directly, due to the mating cue

Assortative mating via pleiotropy seems likely.

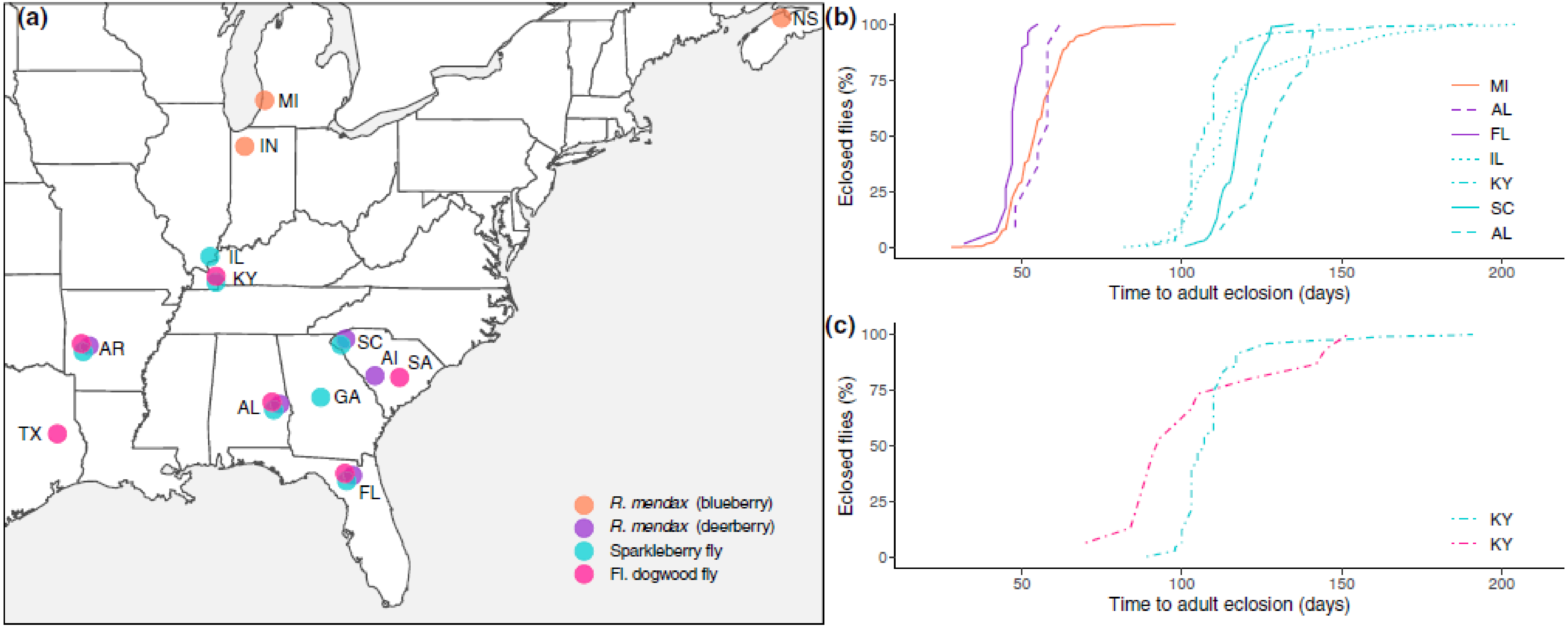
With *m* = 6% gene flow, and no known fixed differences between species, many deny that the apple and haw races have speciated

But if this kind of sympatric evolution (or almost-speciation) can occur in a few tens of years, could be an extremely important over geological time

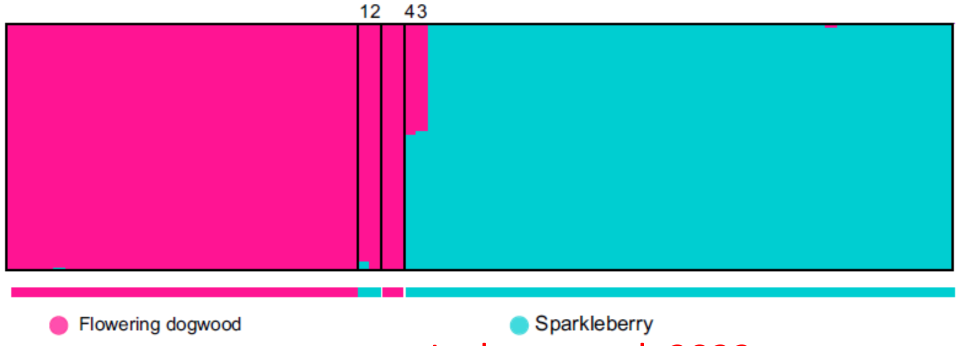
R. pomonella species group



(adapted from Berlocher *et al.* 2000; Xie *et al.* 2008; Powell *et al.* in prep)



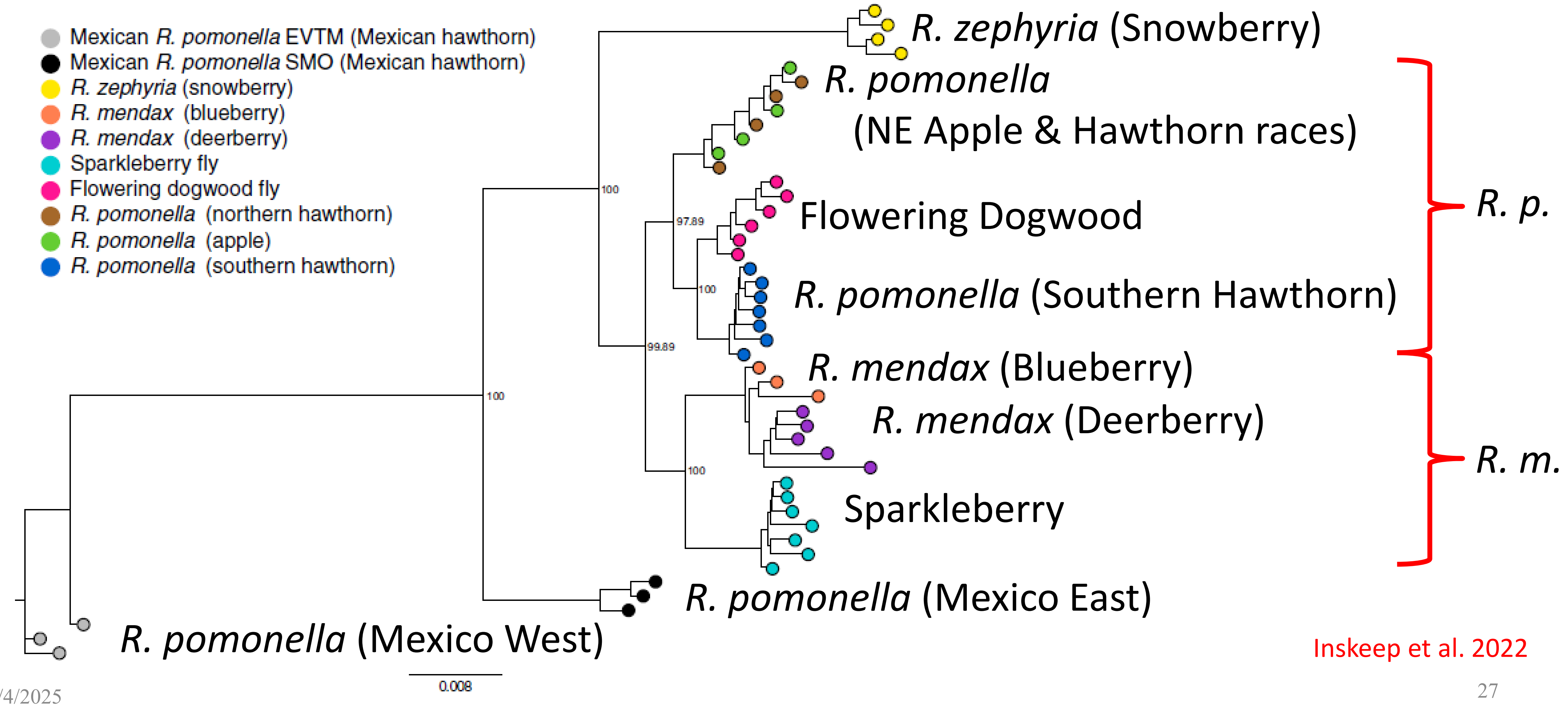
Sparkleberry flies hybridize occasionally with Flowering Dogwood flies in SE USA



Inskeep et al. 2022

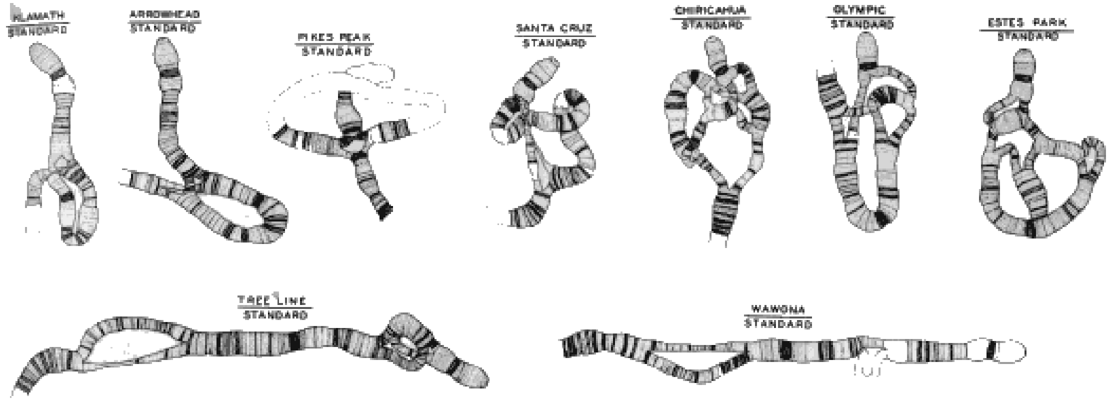
Phylogeny of *R. pomonella* species group

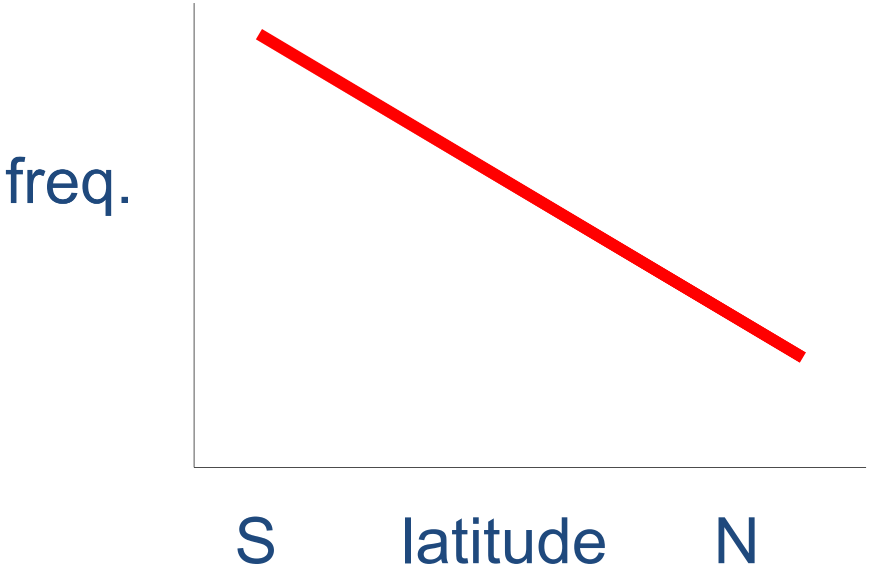
based on reduced representation DNA (ddRAD) sequencing



Inskeep et al. 2022

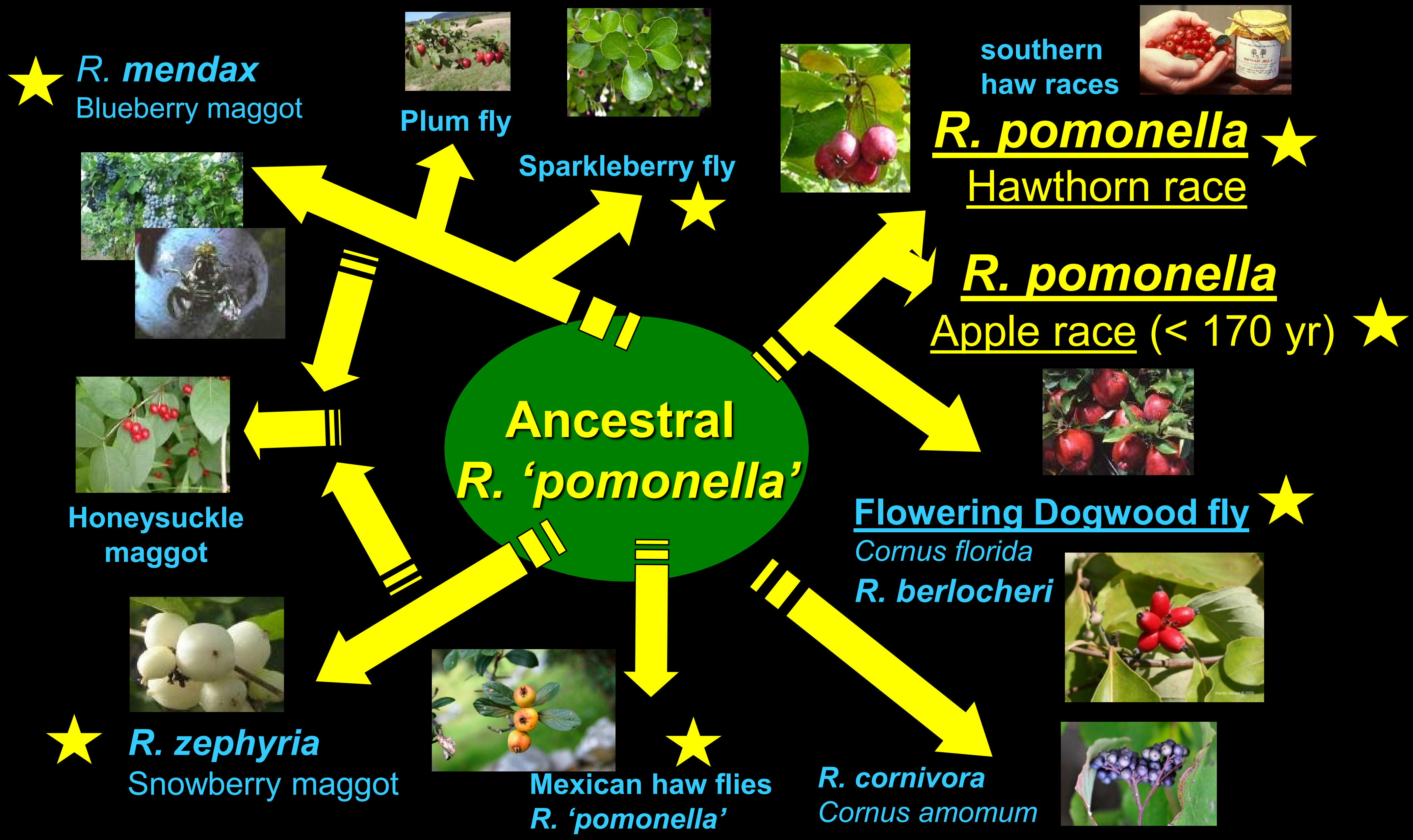
Possibility of chromosome inversions from two sides of Mexico





R. pomonella sibling species complex

whole group speciated via sympatric host shifts (Bush 1966)



Possibility of chromosome inversions from Mexico

- Allele frequencies at allozymes differ between host races, and between different populations of same species or race (e.g. N-S in *R. pomonella*)
- Some evidence for differences across the Sierra Madre in Mexico
- => Feder et al. argue that inversions arose in "allopatry", and contributed to the variation that allowed the sympatric species

Coyne & Orr 2004 pp. 159-162:

- Maybe genetic similarity of apple & haw race due to hybridization
- Maybe the allopatric evolution of chromosomal races was necessary for the formation of the host races and species in *R. pomonella* group
- "Hence, the races of Rhagoletis pomonella may represent not sympatric host-race formation, but an early stage of "allo-sympatric speciation."

Should host races in the apple maggot be considered “good species?”

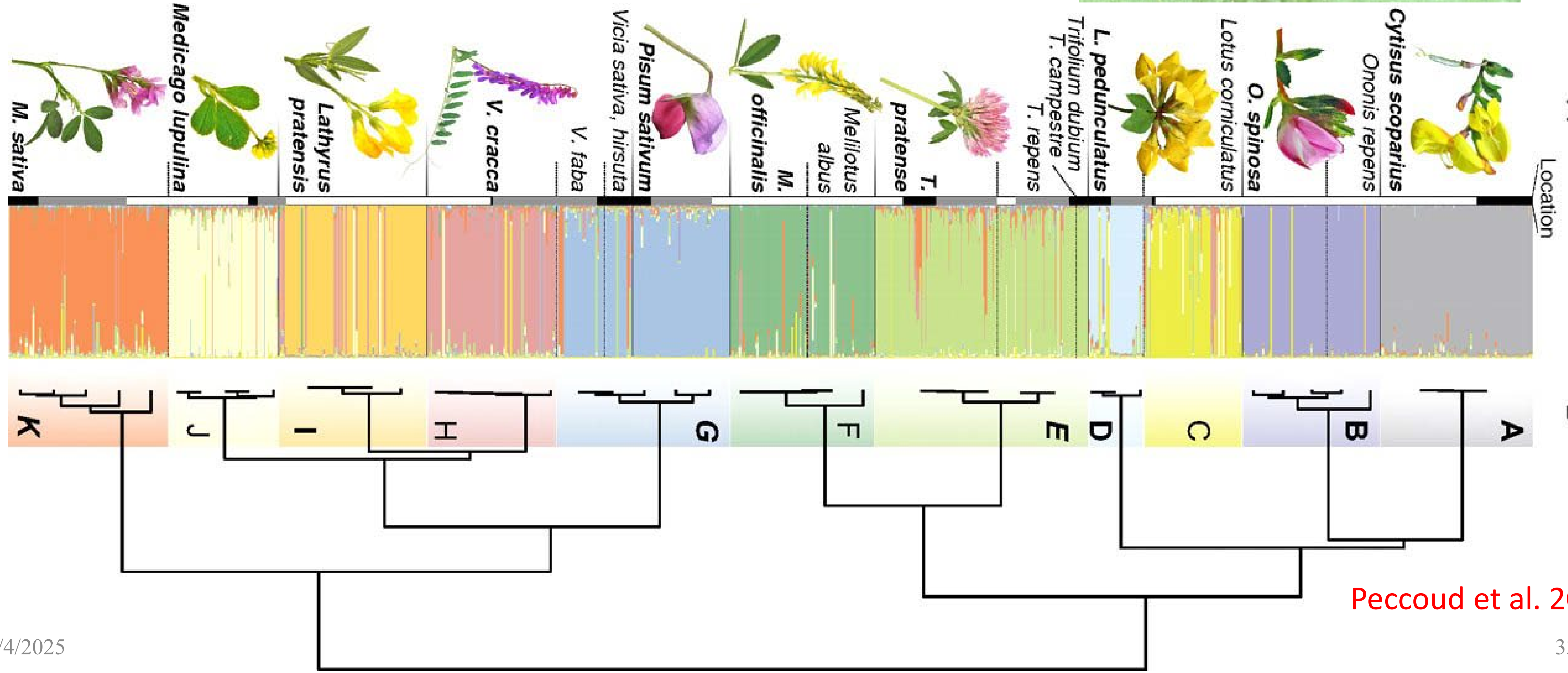
Is the case important for understanding the likelihood sympatric speciation is possible?

I think so! To both questions.
But Coyne & Orr (2004) are more negative about this.
What do you think?

Other examples of ecological races

- Other plant-feeding insect host races
- Fish benthic vs. limnetic morphs (*Stickleback*, *whitefish*, salmonids, etc.)
- Parasite races (e.g. head louse vs. body louse, *Pediculus*)
- Shore snails, upshore & downshore; exposed vs. unexposed forms (e.g. *Littorina*)
- Crossbill biotypes (c.f. Craig Benkman)
- Bottlenose dolphin sympatric morphotypes (*Tursiops*)
- Resident vs. transient killer whales in Prince William Sound, Alaska (A.R. Hoelzel)
- Batwa ("pygmies") of the Bwindi Impenetrable Forest, Uganda hunter gatherers, and traditional servant class of the local Bantu-speaking peoples

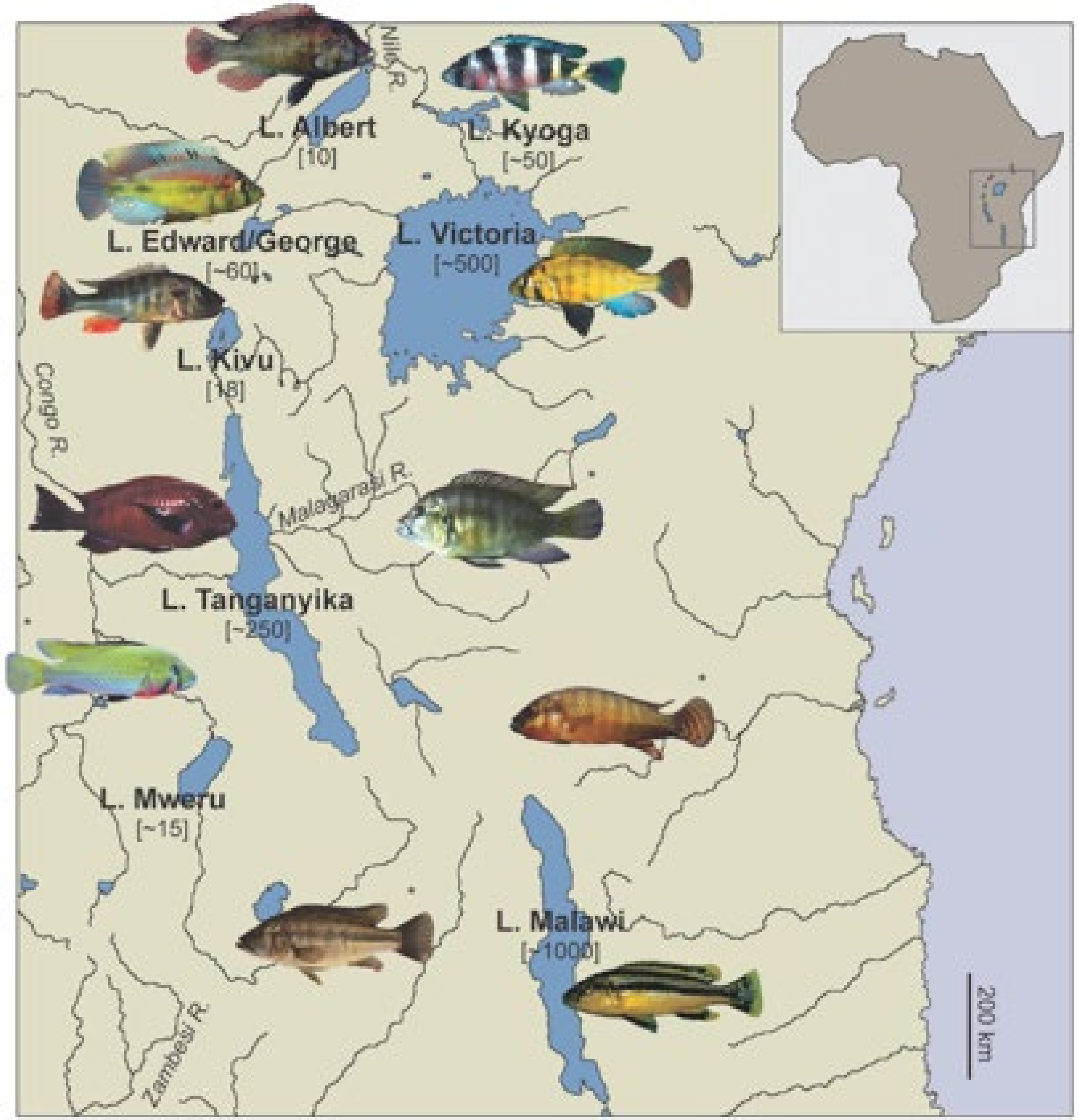
Host races/species in the pea aphid complex *Acyrthosiphon pisum*



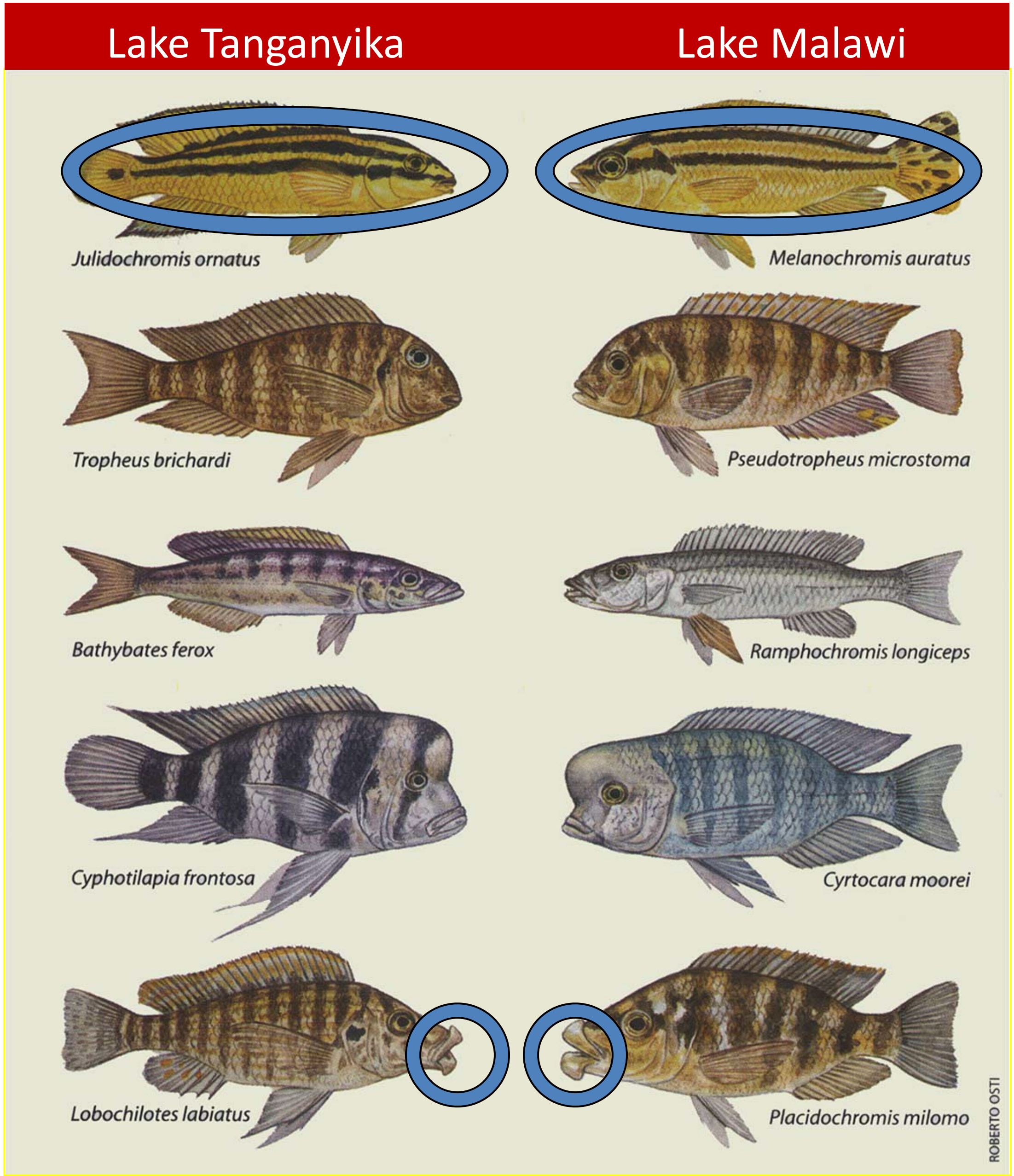
Peccoud et al. 2009

Three large adaptive radiations of cichlid fishes

(Victoria – only 14,000 years old - endemic species 500; Malawi – 800 species; Tanganyika – 250 species)

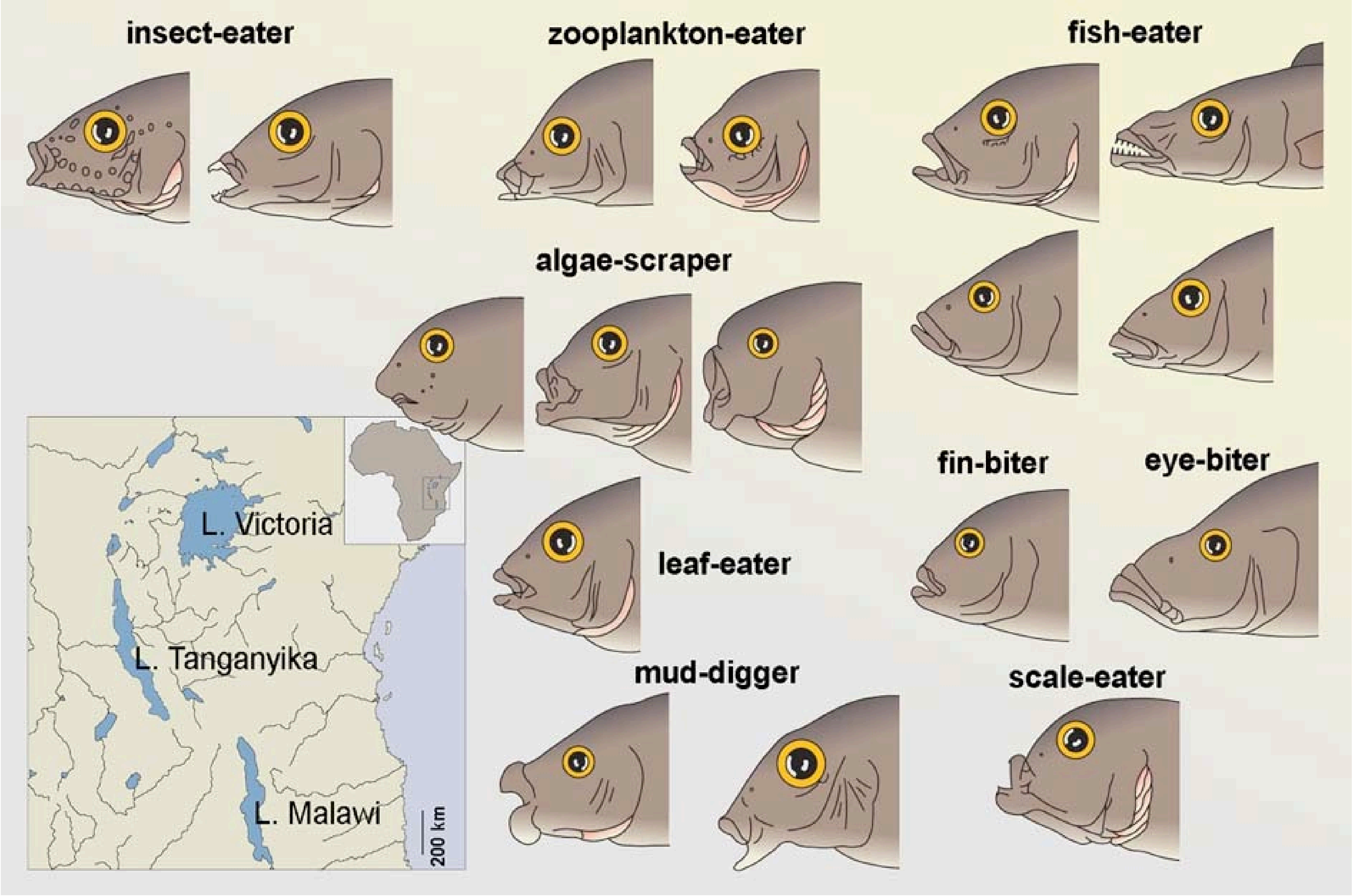


Convergence in cichlid fish adaptive radiations
Determinism, contingency, predictability



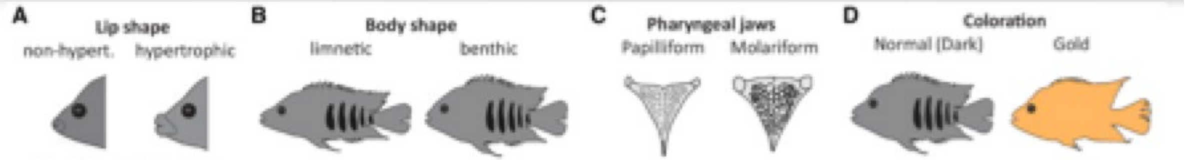
Stiassny & Meyer (1999) *Scientific American*

Trophic adaptations in the three East African species flocks



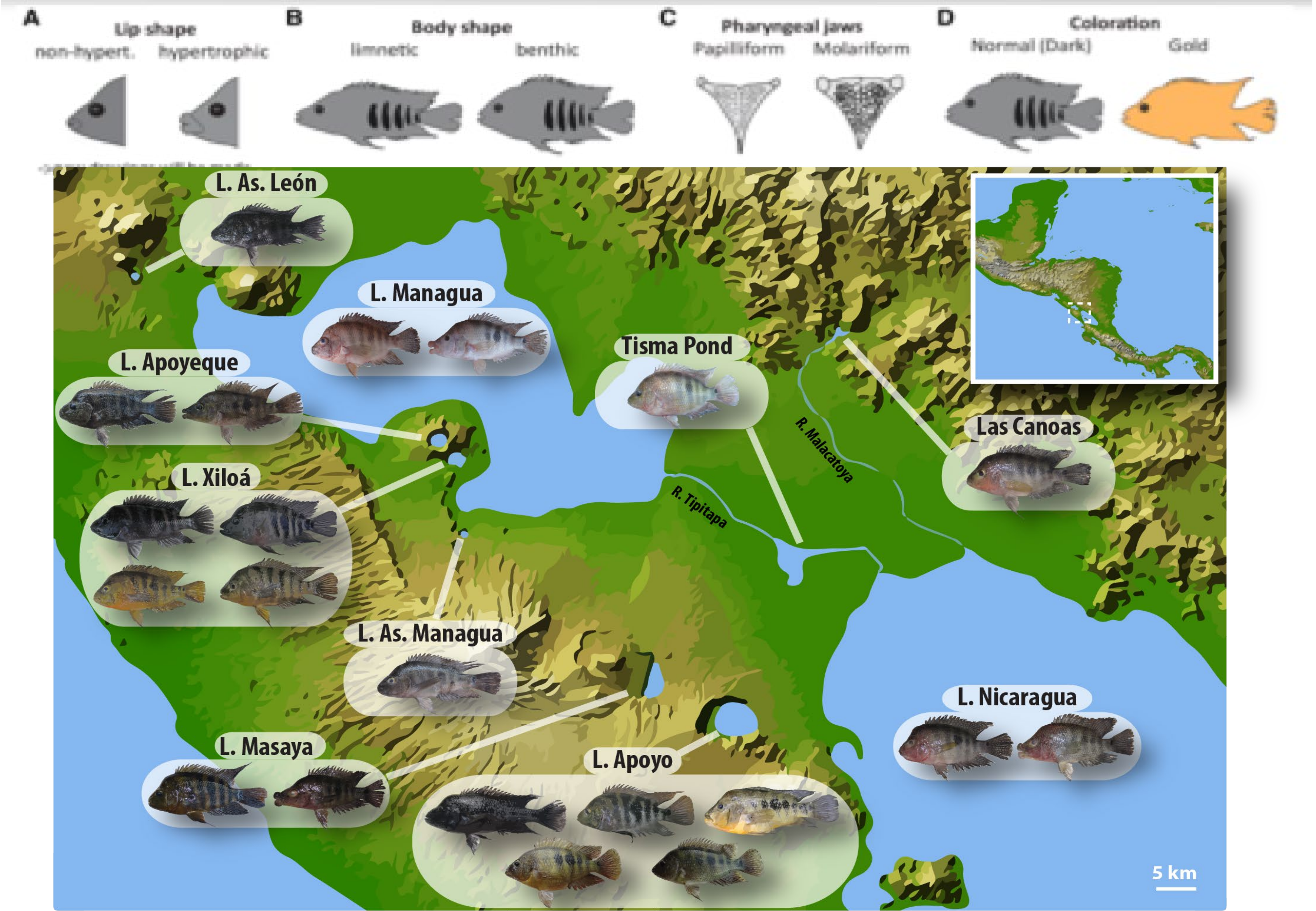
Diversity of the Midas cichlid species complex in Nicaragua

13 described species + polymorphisms

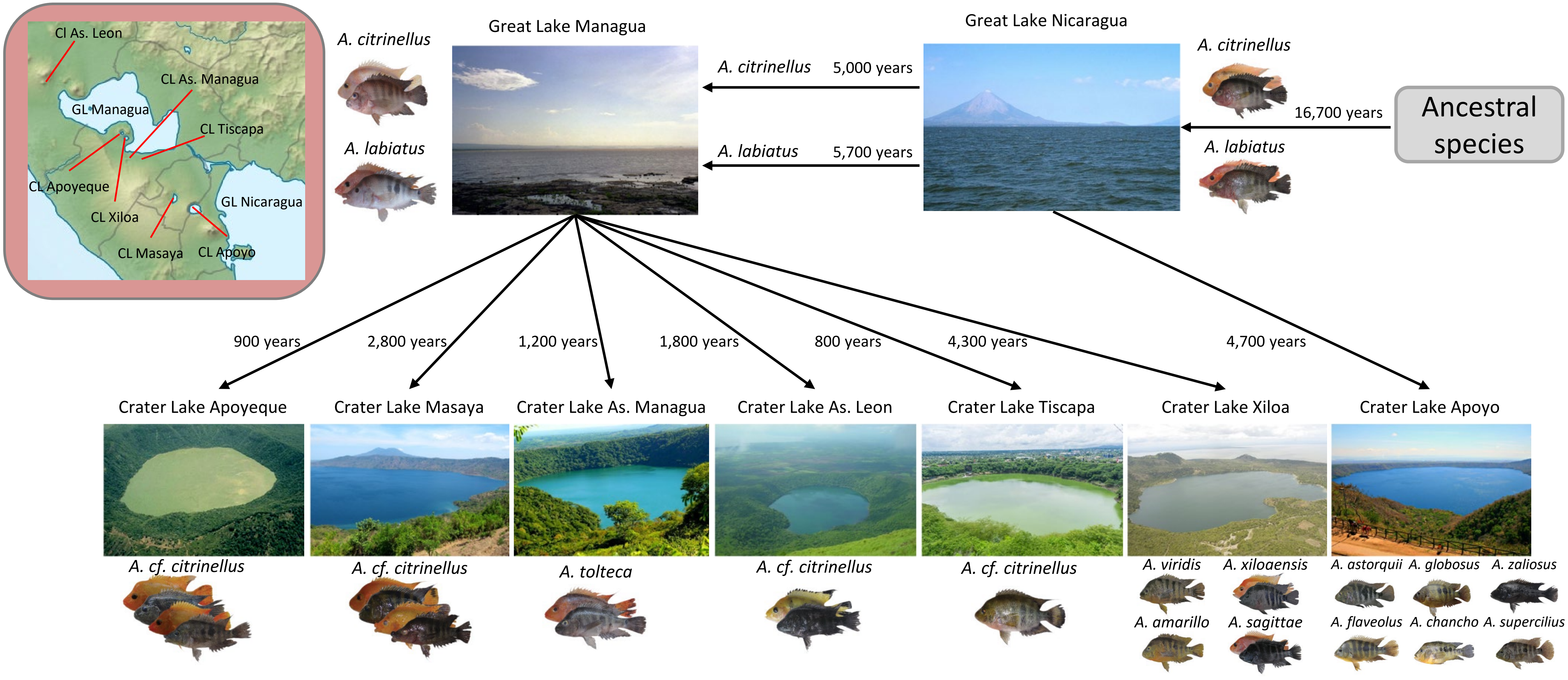


A number of species and forms restricted to small crater lakes

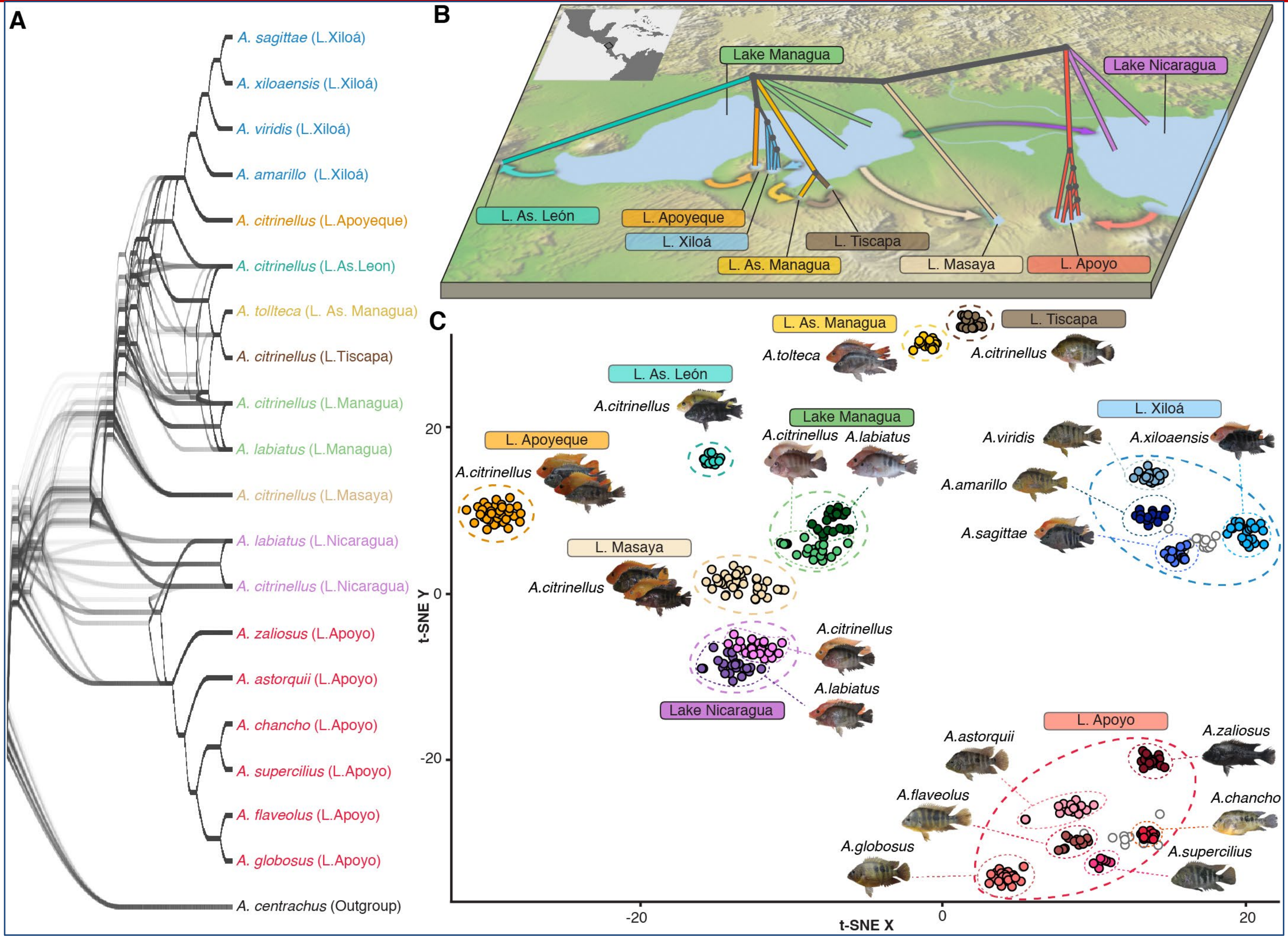
4 major axes of phenotypic differentiation and geographic distribution of the Midas cichlid species complex in Nicaragua



Diversity and distribution of the Midas cichlid species complex in Nicaragua

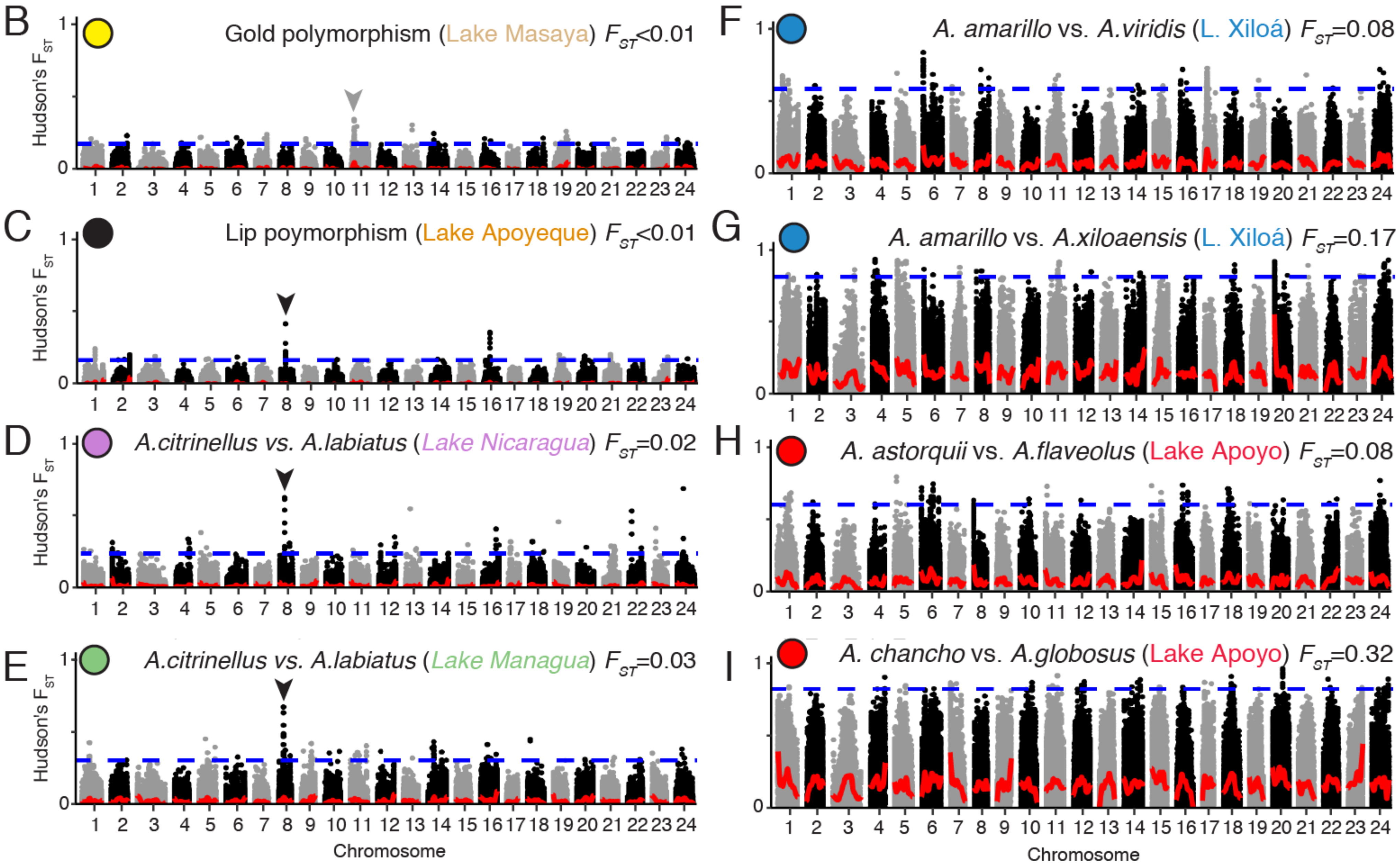


Evidence for sympatric speciation in Nicaraguan crater lake cichlid species flocks: phylogeny, colonization history and population differentiation



Kautt et al. (2020) *Nature*

Genome-wide differentiation and speciation:
Gold and Lips remain polymorphisms, body shape and teeth lead to new species



Kautt et al. (2020) *Nature*

Orcas: “resident”, “transient” and “offshore”

Orcinus orca A diversified portfolio KILLER WHALES *Ecotypes & Forms*

1

A large (perhaps to 9.5 m/31 ft.), black and white form; it migrates to Antarctica during the austral (southern) summer where it forages in open (ice free) waters and feeds mainly on minke whales and occasionally elephant seals. During the winter, it probably migrates to lower latitudes, perhaps to the tropics.

2

A large, two-toned gray and white form with dark cape pattern and very large eye patch. Often has yellowish cast due to diatoms. Circumpolar, it forages mainly in loose pack ice where it preys on ice seals (prefers Weddell seals), which groups wave-wash off ice floes by creating waves with their tails; occasionally takes minke whales.

3

A medium-sized, two-toned gray and white form with a dark cape pattern and large white eye patch. Often appears yellowish due to diatom infestation. Common around Antarctic Peninsula, especially in the Gerlache Strait. Preferred prey unknown but has been seen feeding on penguins on numerous occasions.

4

The smallest killer whale known – adult males reach only 6 m (20 ft). A two-toned gray and white form with a dark gray cape; often colored yellowish by diatom film. Eye patch is distinctively narrow and slanted. Occurs deep in the pack ice in eastern Antarctica and feeds on fish; especially common in the Ross Sea.

5

Recently described form, known from perhaps a dozen sightings. Easily recognized by its tiny eye patch (all ages); head is rounded, dorsal fin often swept back and pointy. Distribution circumglobal in subantarctic waters (north of 60°S); sometimes associated with islands. Preferred prey unknown but reportedly steals fish off longlines.

6

The best-known killer whale. A medium-large (to 7.2 m), black and white form that lives in coastal waters of the North Pacific. Saddle patch often has a large black intrusion ('open' saddle) not found in other killer whales. A fish-specialist – some populations feed almost exclusively on salmon. Females may live to 80-90 years.

7

A large (perhaps 8 m), black and white form – similar to resident killer whale except it lacks an open saddle. Occurs in coastal and offshore waters of the North Pacific. A mammal-eater, it feeds mostly on harbor seals and minke whales but will also take sea lions, otters, calves of large whales, etc. Named after pioneer killer whale researcher - Michael Bigg.

8

A smaller form (to 6.7 m) rarely observed because it occurs mainly over outer continental shelf of eastern North Pacific. Group size usually large (100-200); ranges widely: some groups travel between Alaska and southern California. Apparently feeds extensively on sharks and teeth are often worn to gum line due to rough skin of sharks.

9

A smaller (to 6.6 m), black and white form, currently known only from the North Atlantic. Off Norway, feeds on herring and mackerel, which are cooperatively herded into dense schools; some individuals have also been seen to take seals. Teeth of this form are often worn smooth to the gum line – perhaps from feeding on sharks also.

10

A large (to 8.5 m), black and white form (only recently recognized), but with a distinctive back-sloping white eye patch. Few recorded observations, but currently known only from the North Atlantic where it is known to prey on other cetaceans, especially minke whales.

The killer whale (*Orcinus orca*) occurs in all the world's oceans where it is *the* top marine predator and perhaps the most widespread vertebrate on earth. Although currently considered to be a single, worldwide species, recent research has revealed that there are at least 10 recognizable forms (or ecotypes) of killer whales, which are shown here drawn to scale. For the most part, these forms have different prey preferences, distributions, social structures, foraging behaviors, acoustics, physical features, and genetics. This has led some researchers to suggest that there is more than one species of killer whale, and perhaps several. Our research seeks to understand the taxonomy and role of these predators in marine ecosystems.

http://swfsc.noaa.gov/prd-killerwhale/

Illustration and design: Uko Gorter (www.ukogorter.com) Text: R. L. Pitman, *Southwest Fisheries Science Center, NOAA Fisheries Service*, Robert.Pitman@noaa.gov **Photo credits:** R.L. Pitman (1,2,4,7); John Durban (3,6); Paul Tixier (5); Paul Wade (8); Andy Foote (9); Lewis Drysdale (10)

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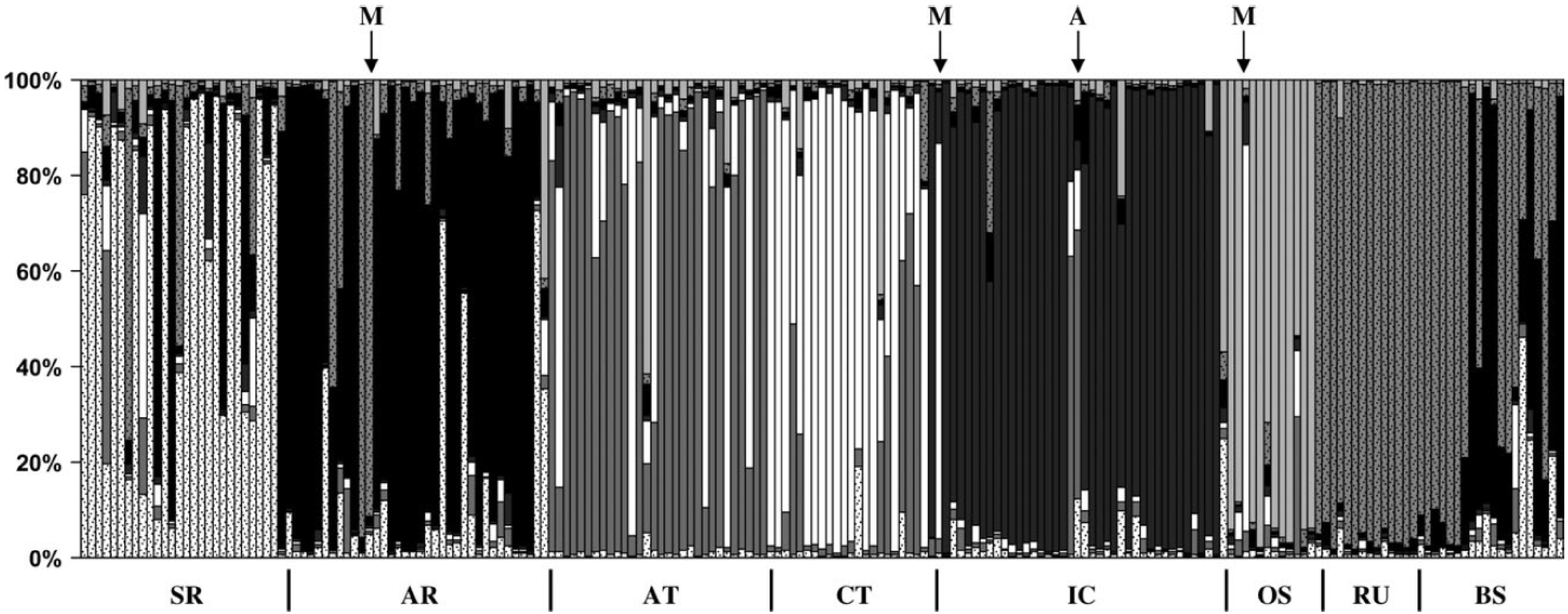
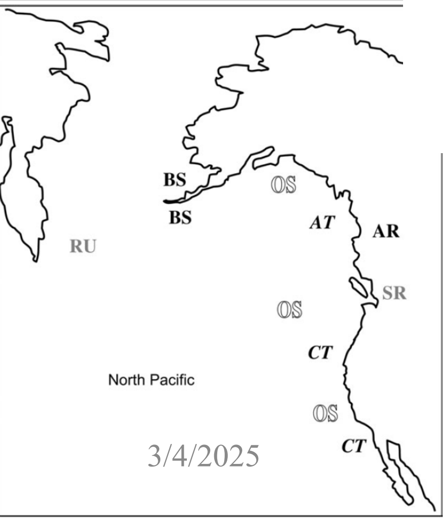
Orca population structure in the N. Pacific

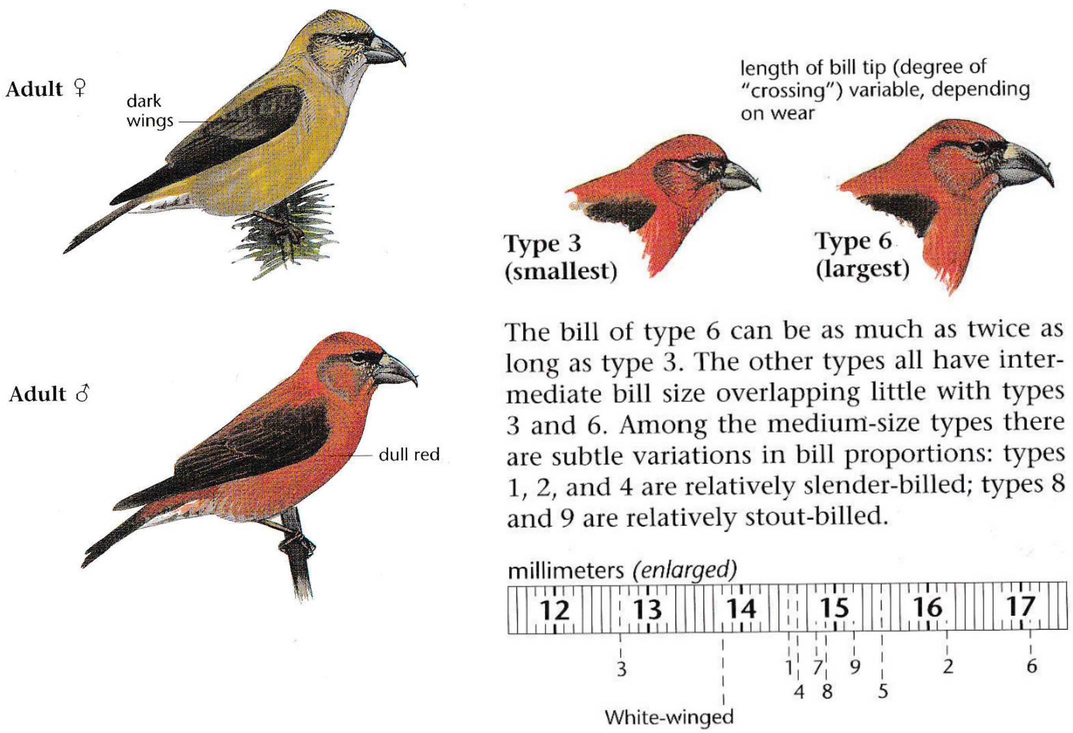




SR = southern resident, RU = Russian residents, AR = Southeast Alaskan resident, BS = Bering Sea residents, OS = offshore, AT = Southeast Alaskan transients, CT = Californian transients, IC = Iceland.

Hoelzel et al. 2007

Crossbill ecotypes (*Loxia curvirostra* complex)



Sibley's birds

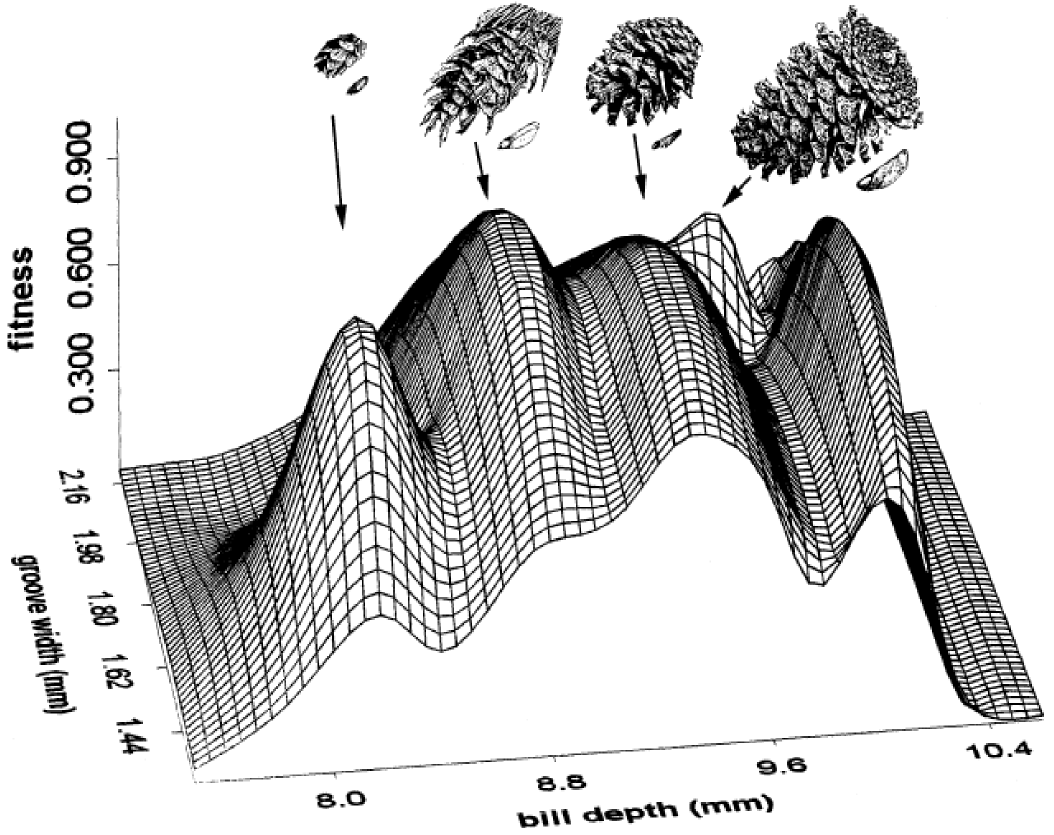
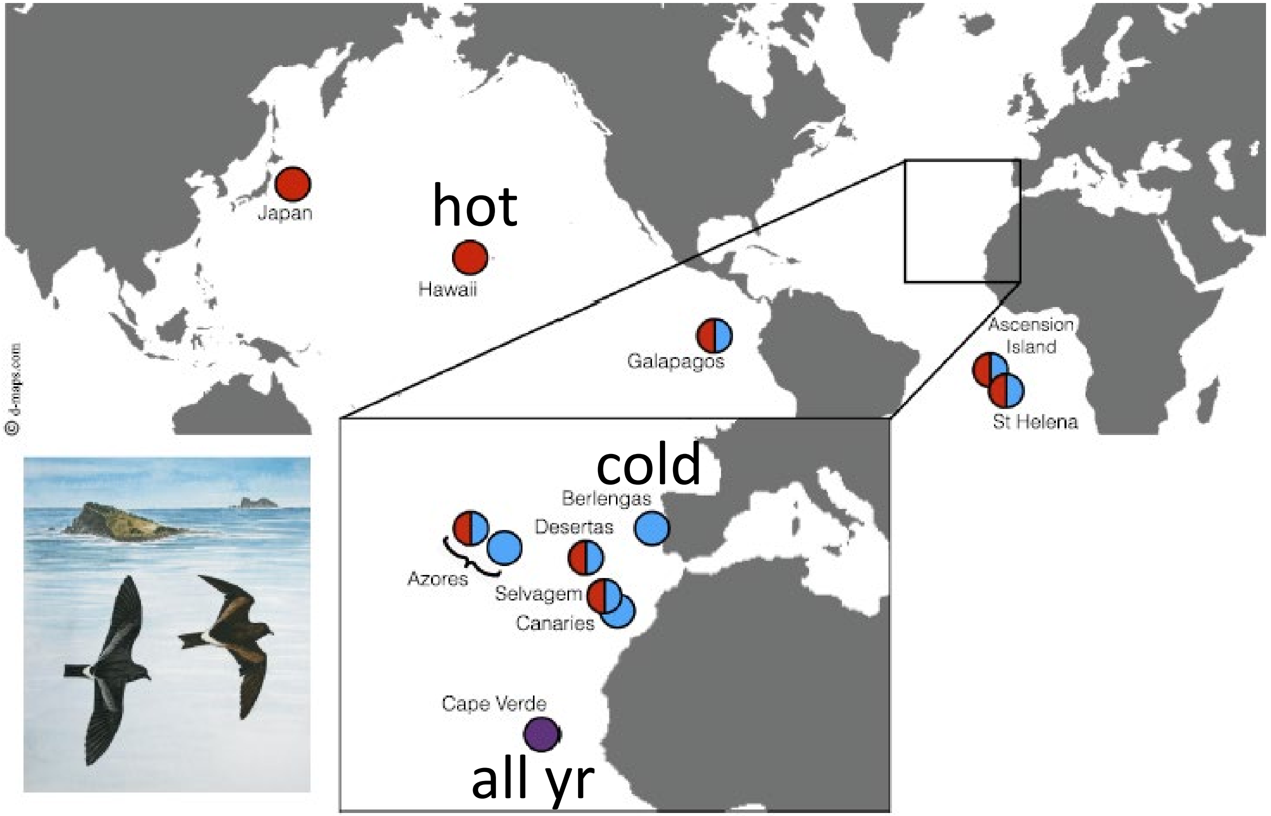
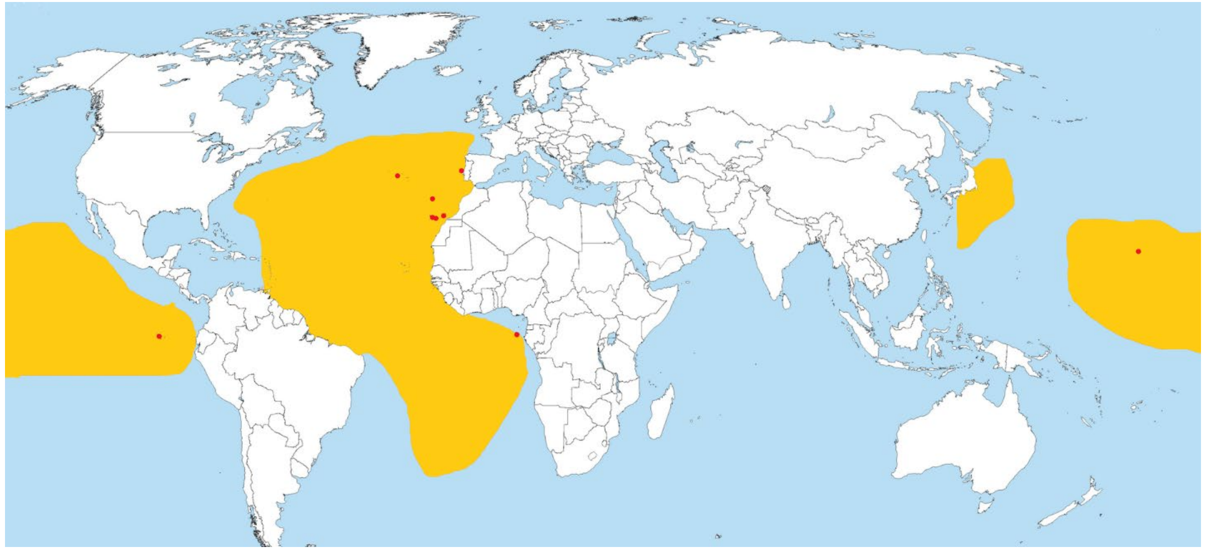


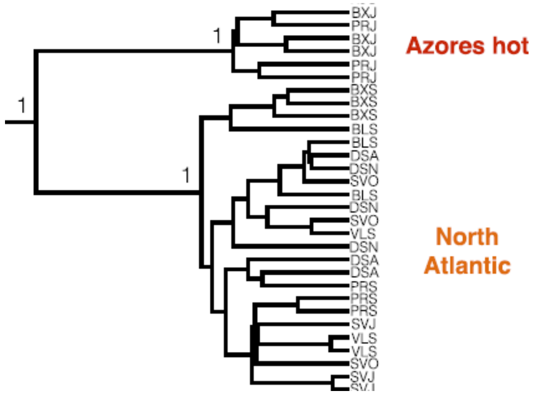
FIG. 3. A fitness surface for five different red crossbill taxa based on foraging data from the laboratory that was converted into fitness (survival) using the relationship between feeding efficiency and survival (Fig. 2). The adaptive peaks correspond to the following conifers from left to right: western hemlock, Douglas fir, Rocky Mountain lodgepole pine, ponderosa pine, and South Hills lodgepole pine, with cones and seeds (with wings) of the first four conifers drawn above to relative scale.

Benkman

Band-rumped Storm-Petrel, *Hydrobates castro*





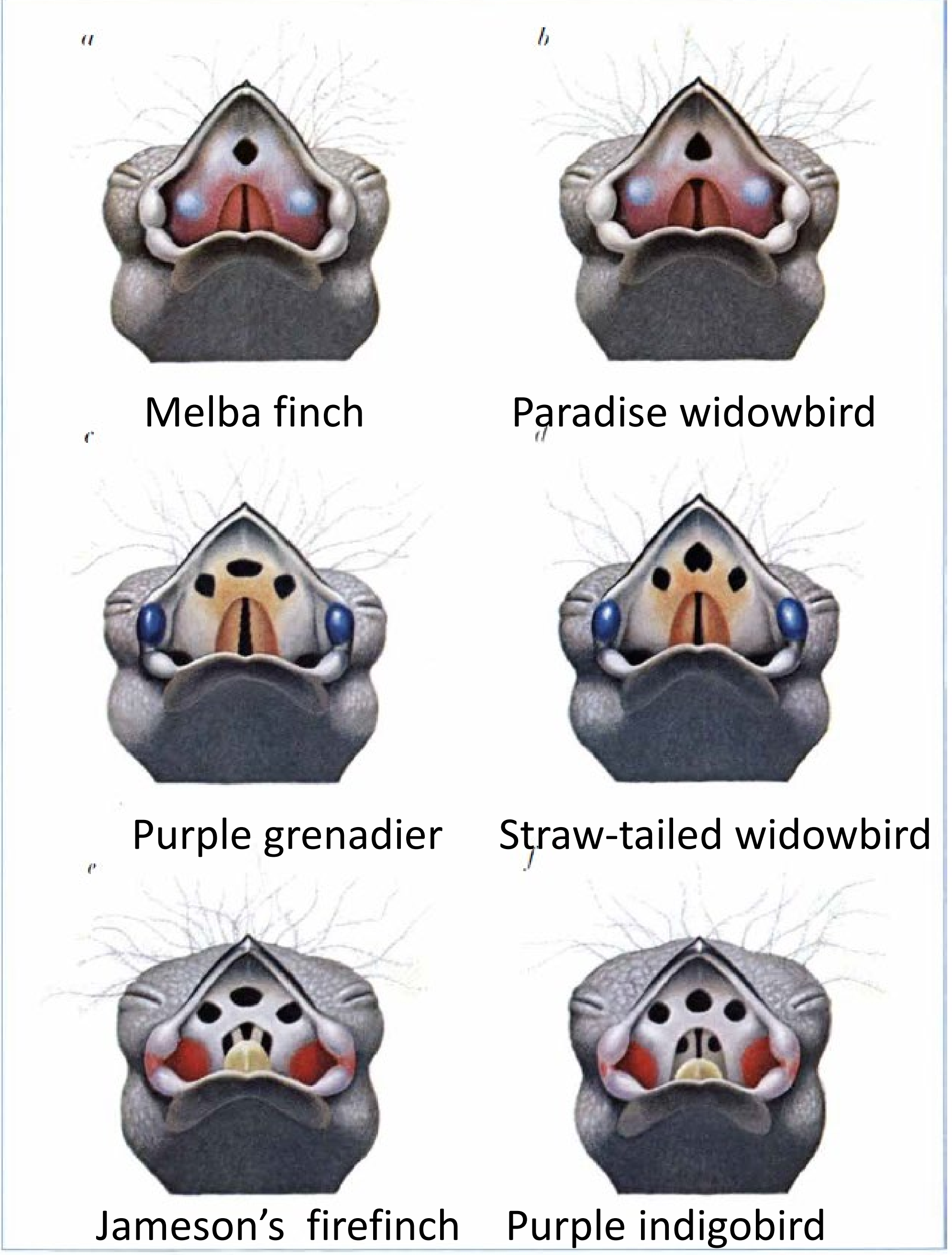


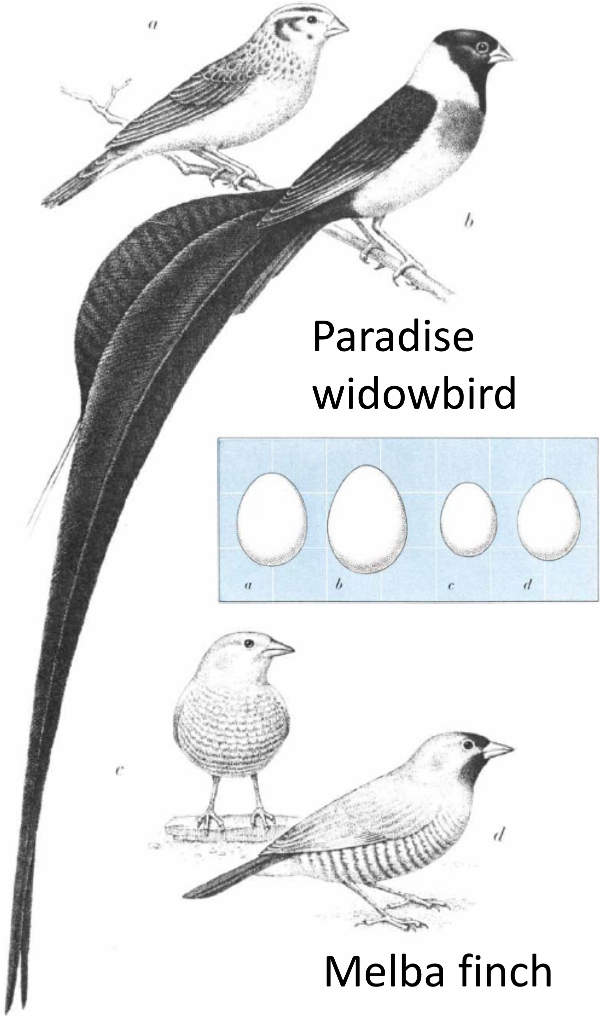
Azores Islands: some birds breed in the hot season (June), others in the cool seasons (Sept, Oct, November).
Separable on the basis of both mtDNA and nuclear genomes
Up to 6 pairs of sympatric allochronic divergent taxa

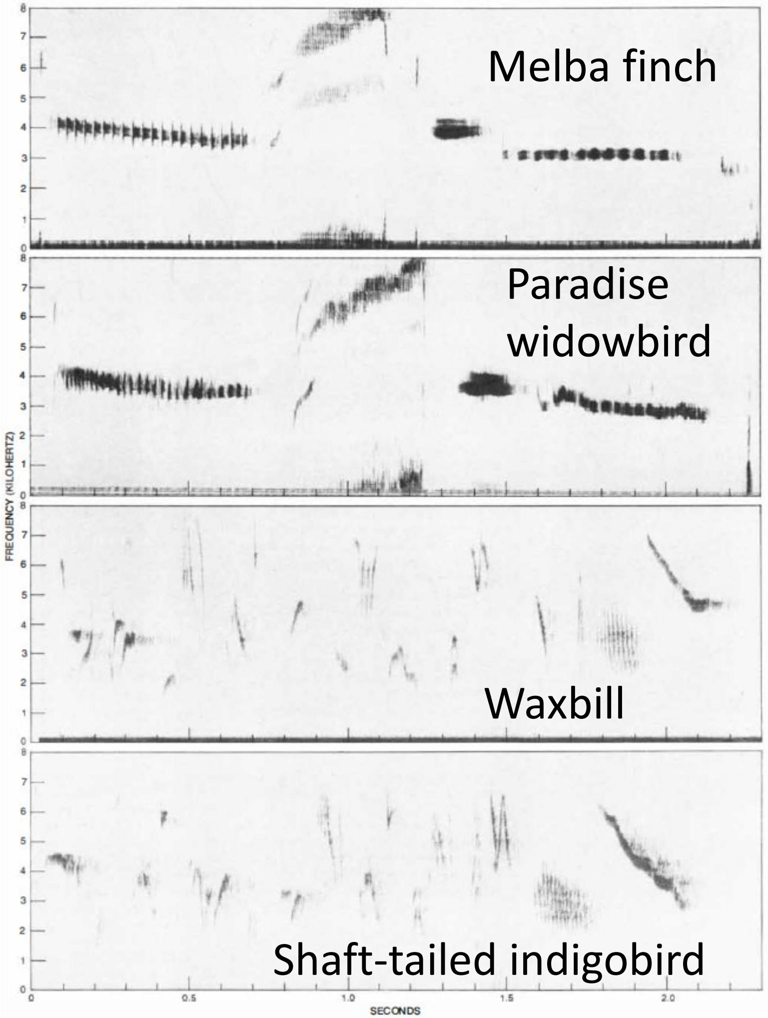
R.S. Taylor et al. 2019

Widow birds and indigo birds (*Vidua*)

Vidua species are egg parasites of estrildid finches







SONG MIMICRY, a meticulous imitation of the host male’s call, learned by the parasite male while a juvenile, is demonstrated by these paired sonograms. The top sonogram shows the final seconds of a Damara melba finch’s song; the sonogram directly below it is mimicry of this part of the finch’s song by a male paradise widow bird. The third sonogram shows a two-second segment of the song of the violet-eared waxbill; the fourth is mimicry of this segment of the song by the waxbill’s parasite, the shaft-tailed widow bird.

Nicolai 1974

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to M.J.T. (mt281@cam.ac.uk). Newly determined sequences have been submitted to GenBank under accession numbers AY291292–AY291293.

Speciation by host switch in brood parasitic indigobirds

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A growing body of empirical and theoretical work supports the plausibility of sympatric speciation[1–3], but there remain few examples in which all the essential components of the process are well understood. The African indigobirds *Vidua* spp. are host-specific brood parasites. Indigobird nestlings are reared along with host young, and mimic the mouth markings of their respective hosts[4–6]. As adults, male indigobirds mimic host song[4–7], whereas females use these songs to choose both their mates and the nests they parasitize[8]. These behavioural mechanisms promote the cohesion of indigobird populations associated with a given host species, and provide a mechanism for reproductive isolation after a new host is colonized. Here we show that all indigobird species are similar genetically, but are significantly differentiated in both mitochondrial haplotype and nuclear allele frequencies. These data support a model of recent sympatric speciation. In contrast to the cuckoo *Cuculus canorus*, in which only female lineages are faithful to specific hosts[9,10], host switches have led to speciation in indigobirds because both males and females imprint on their hosts[8,11].

The high degree of host specificity in indigobirds led previously to the suggestion that host–parasite associations in African finches were the product of a long history of co-speciation[4]. This model

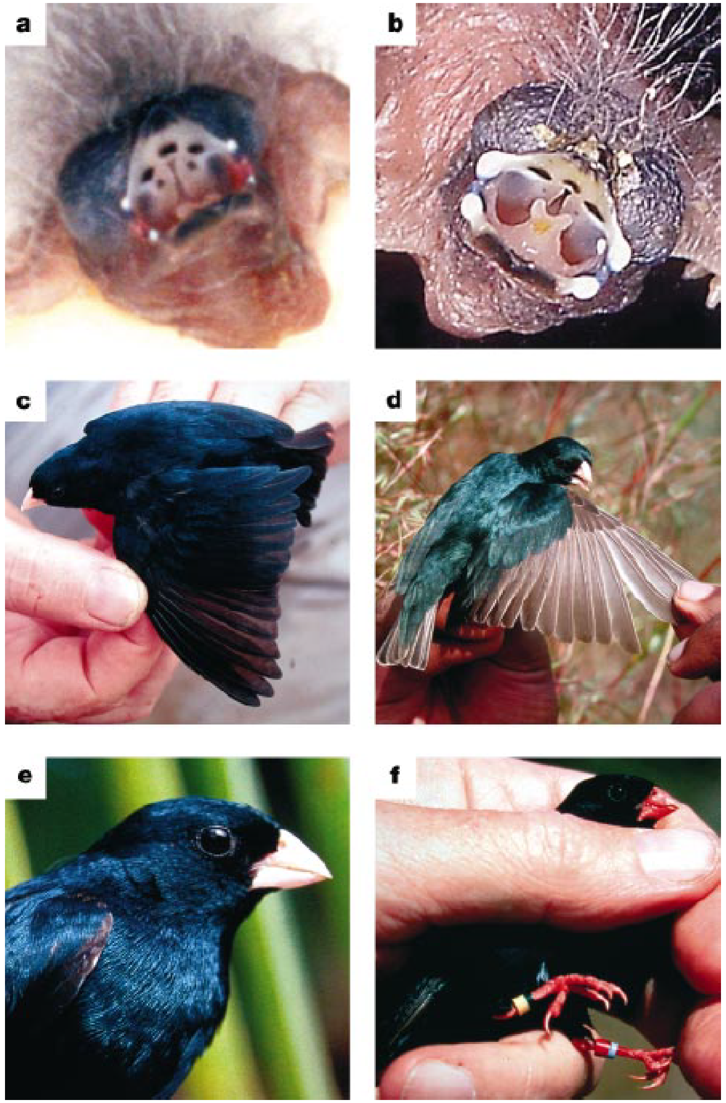
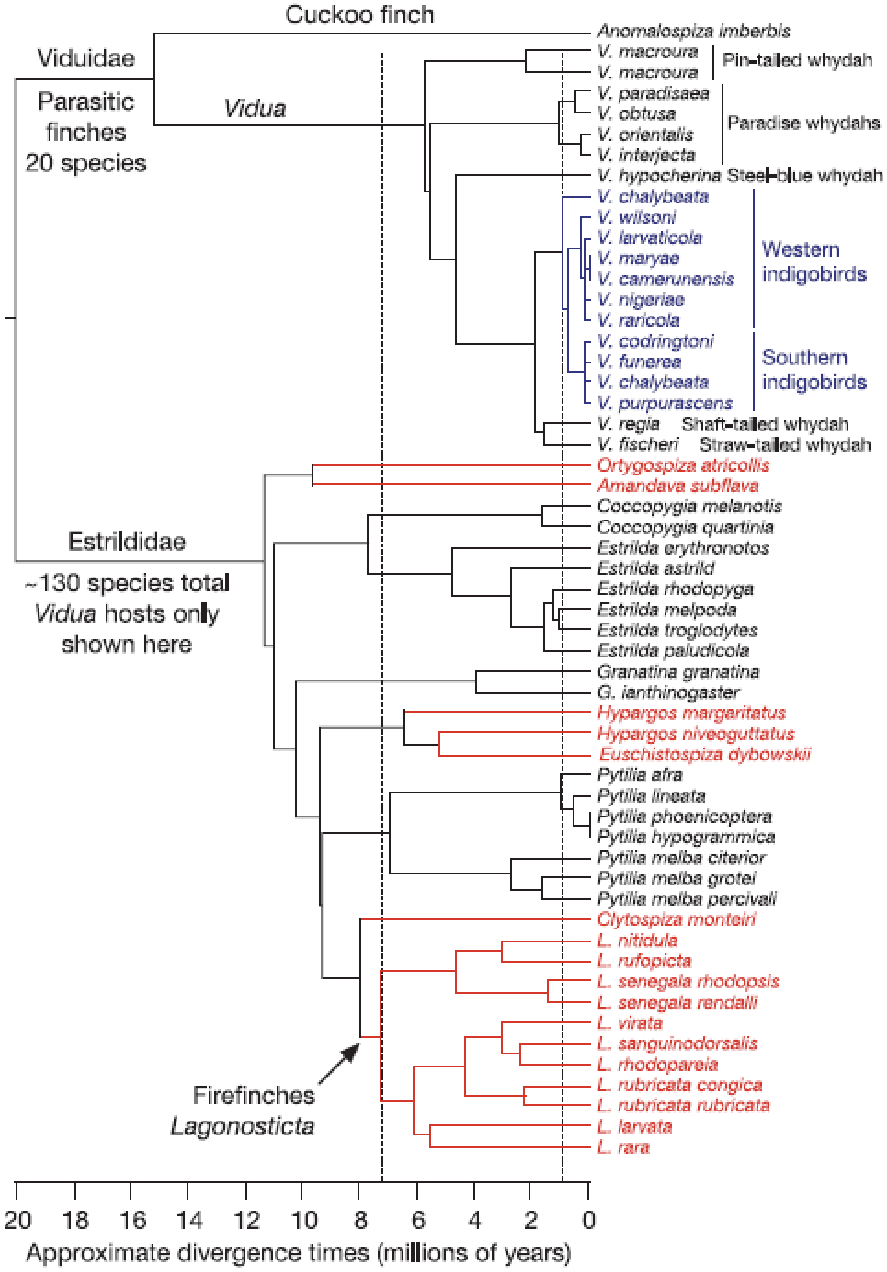
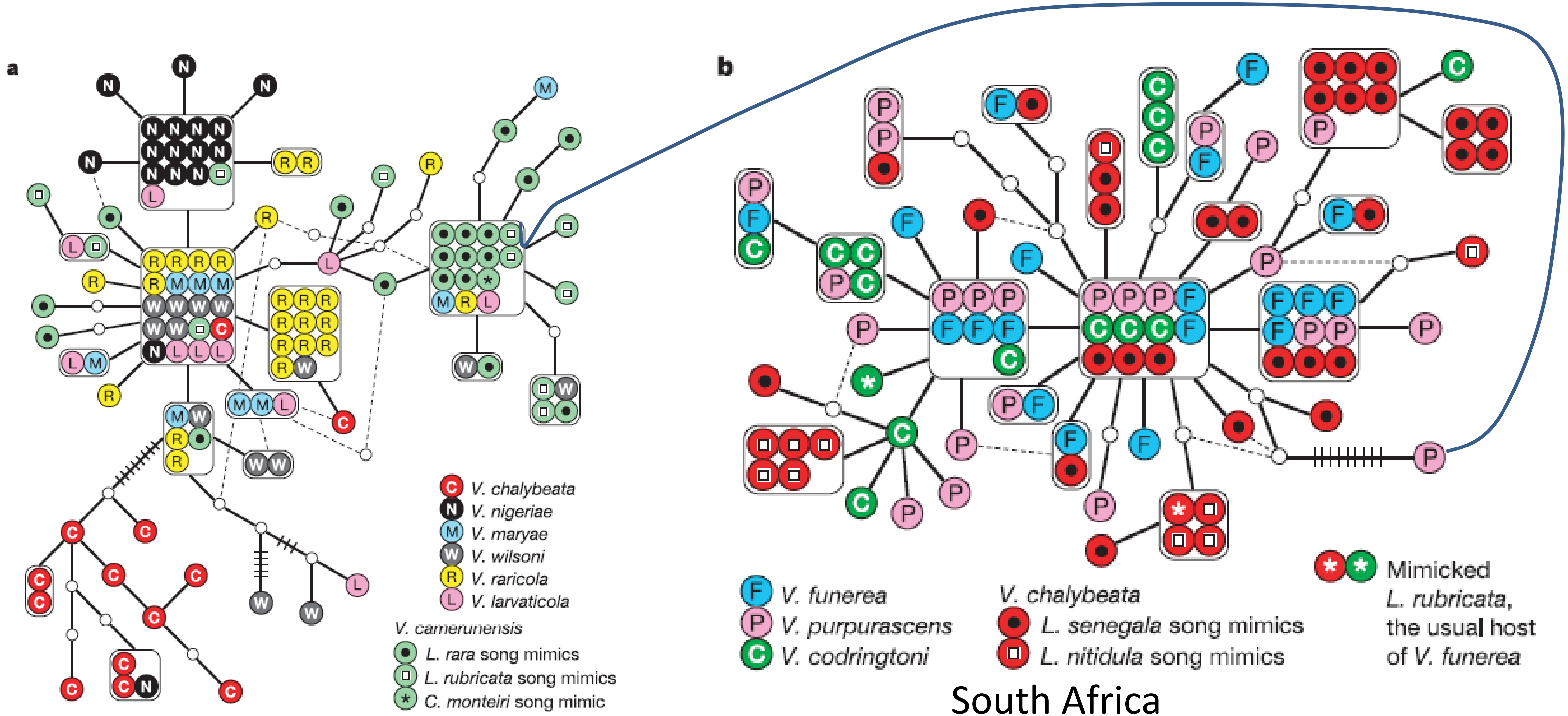


Figure 1 Examples of morphological variation between indigobird species. Nestling mouth markings in *V. camerunensis* (**a**) and *V. chalybeata* (**b**) mimic the young of their firefinch hosts, *L. rara* and *L. senegala*, respectively. Dark wing and plumage in *V. chalybeata* from West Africa (**c**). Pale wing and green plumage in *V. raricola* (**d**). White bill and blue plumage in *V. camerunensis* (**e**). Red bill and orange feet in *V. chalybeata* from southern Africa (**f**). See ref. 30 for a complete description of morphological differences between indigobird species.



Sorensen et al. 2003

Mitochondrial haplotypes of indigobirds

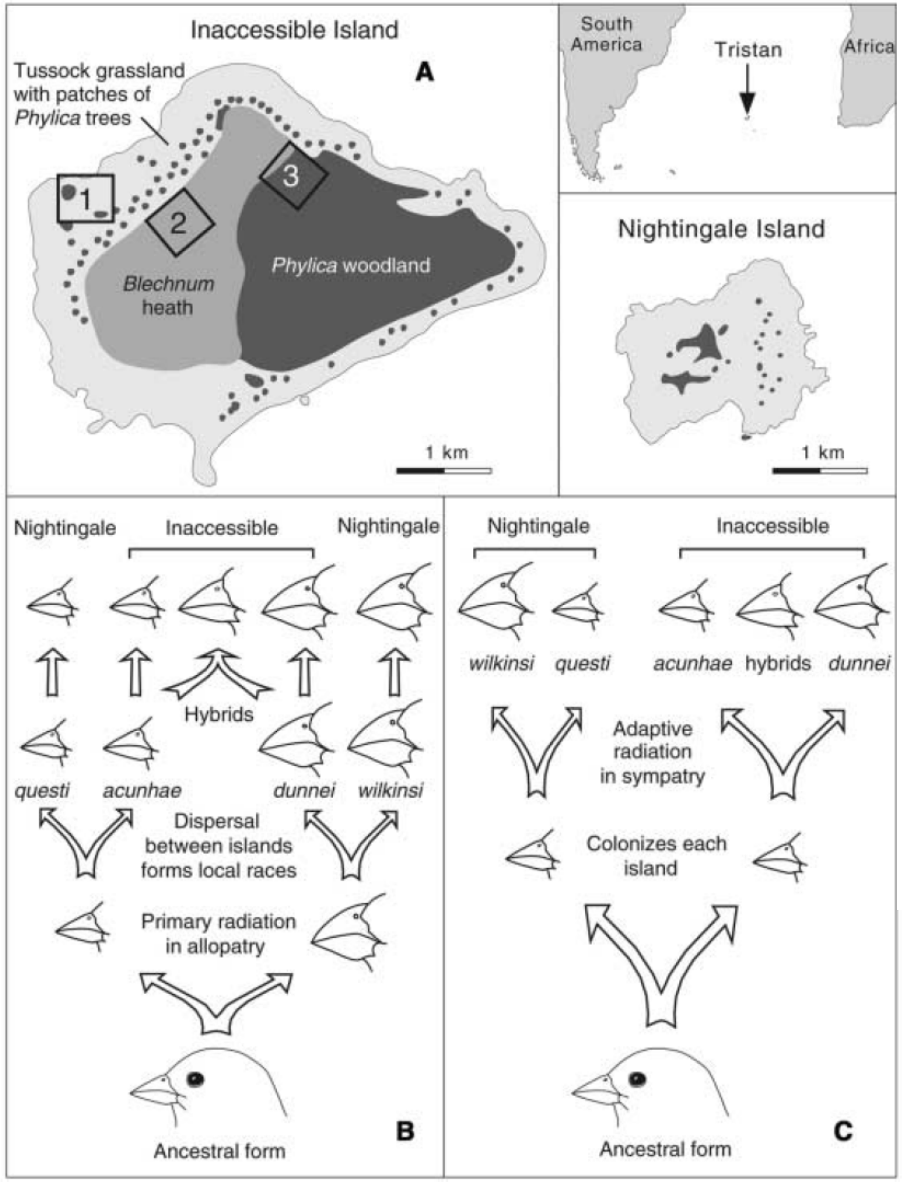


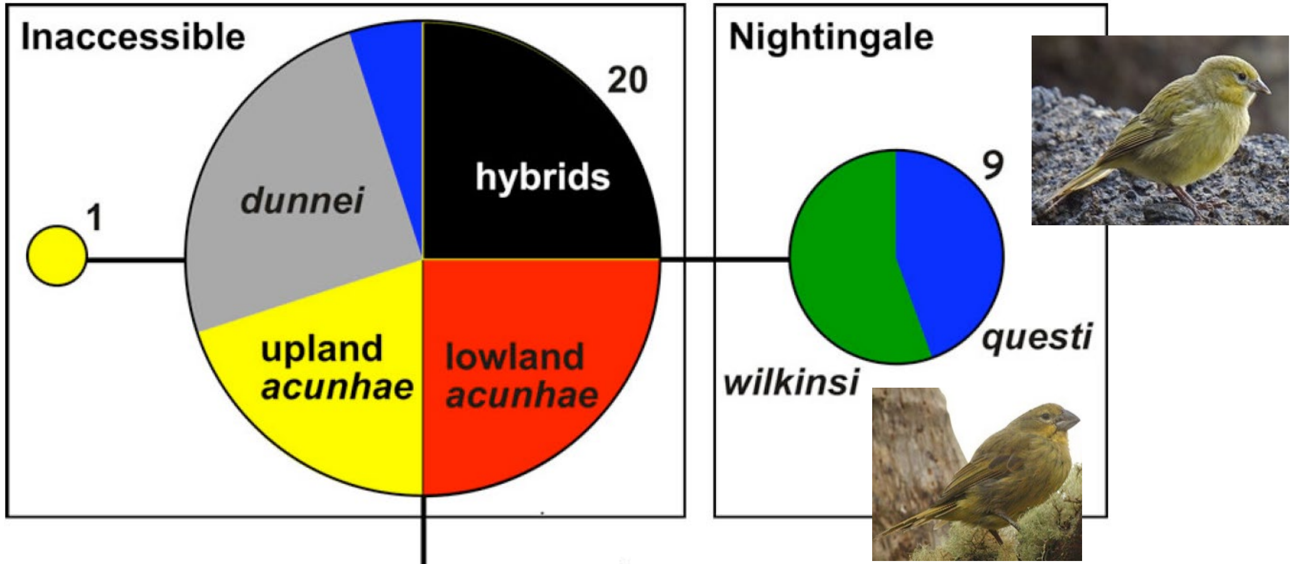
Nigeria and Cameroon

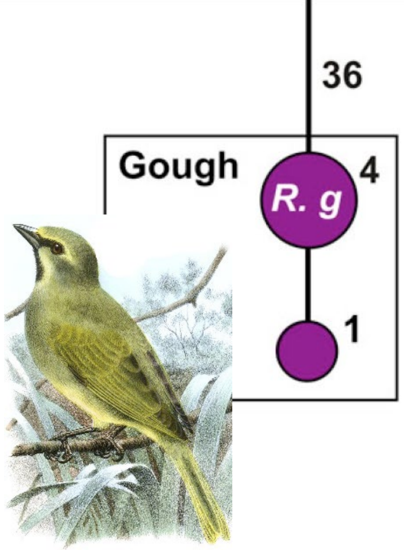
South Africa

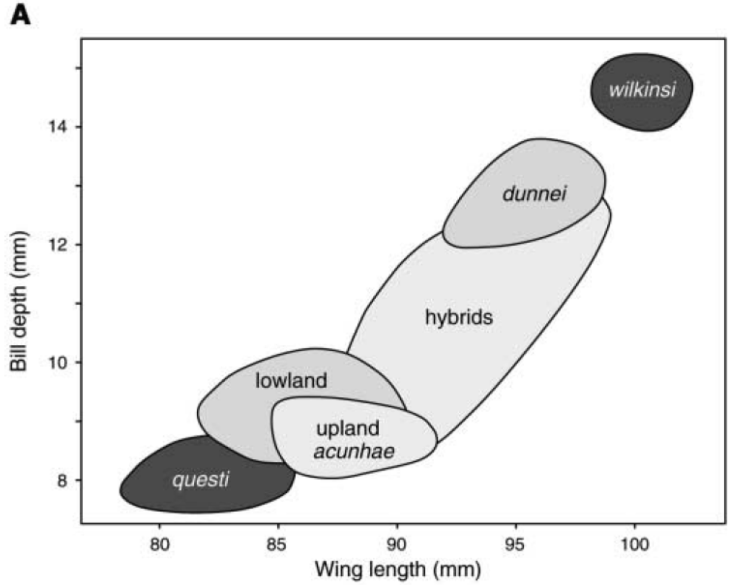
Sorensen et al. 2003

Neospiza buntings, Tristan da Cunha archipelago



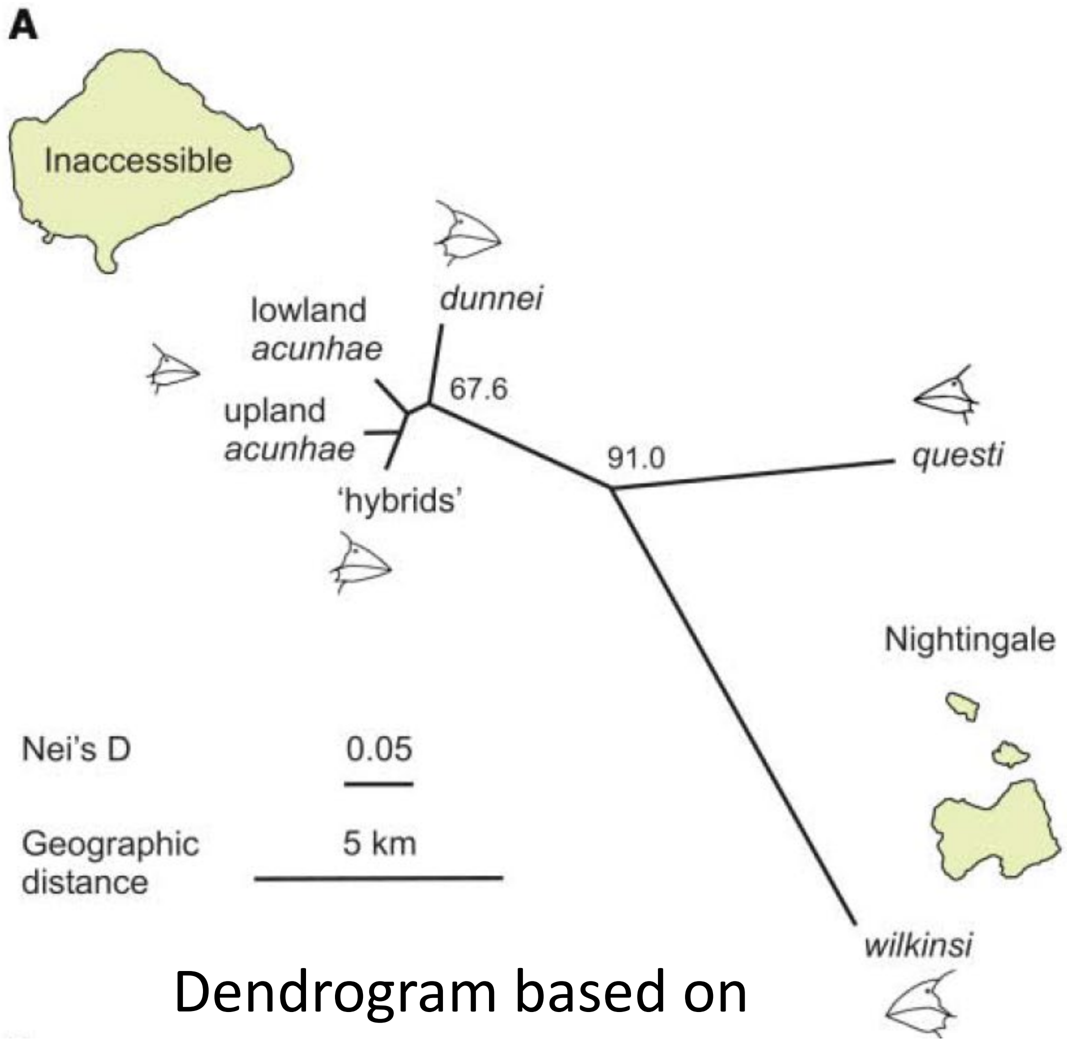




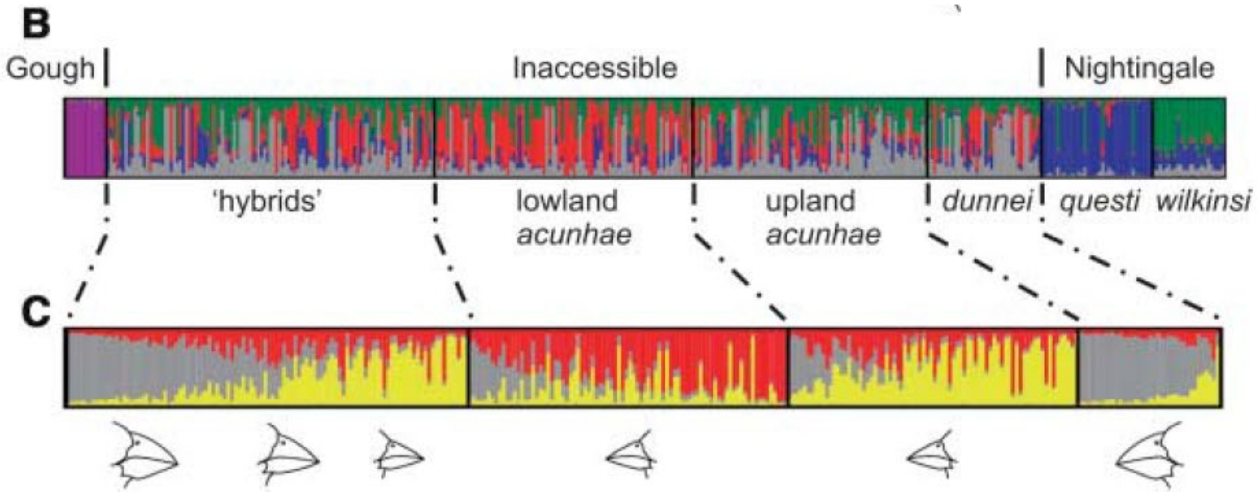


Ryan et al. 2007

More *Neospiza* from Tristan da Cunha



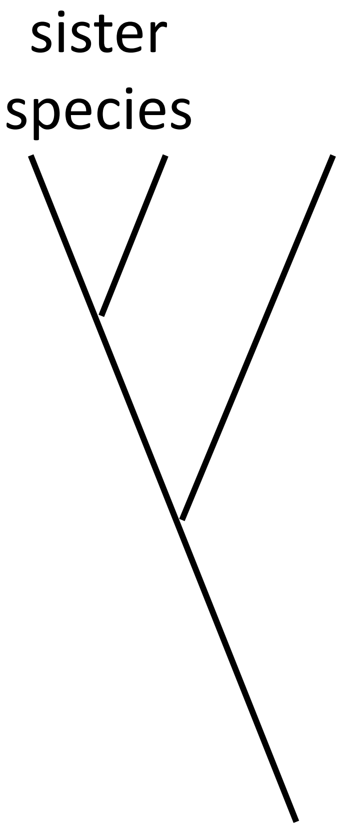
Dendrogram based on microsatellite data



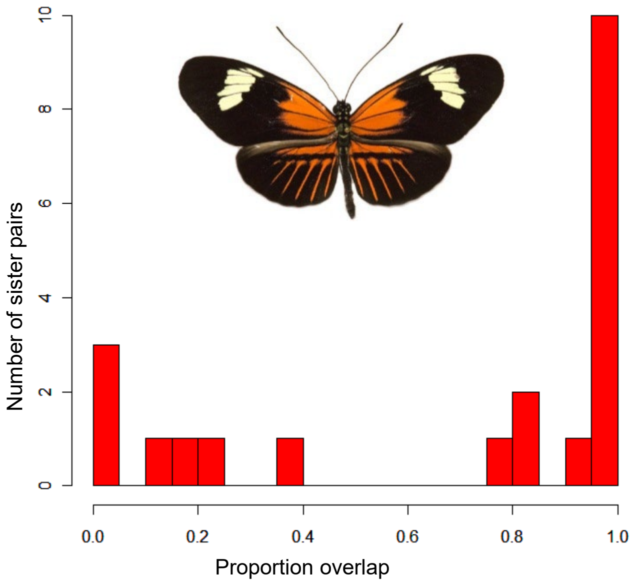
STRUCTURE assignment analysis based on microsatellites

Ryan et al. 2007

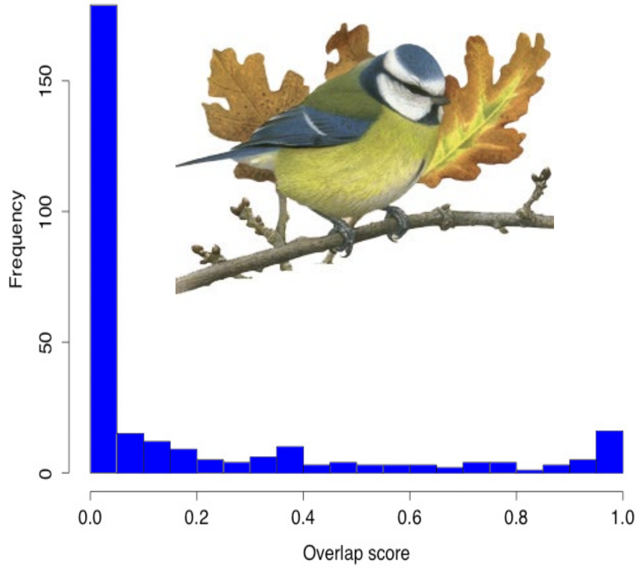
Range overlap between sister species



Heliconius



Birds



Neil Rosser, Ally Philllimore et al. 2012

Sympatric speciation

Common or rare:
What do you think?

Is it even a sensible question to ask?