MCB 291 Genetics, Genomics and Evolution

The speciation continuum: ecological races

Today:

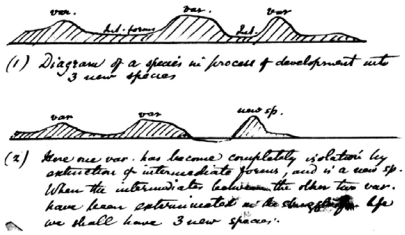
How close are populations within species to being species?

1

Intermediates between species: geographic subspecies

AR Wallace, 29 Nov 1900, letter to H.M. Bernard:

"Definition of a Species: A species is a group of individuals which reproduce their like within definite limits of variation, and which are not connected with their nearest allied species by insensible variations."



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Darwin's supposed "Failure"

"Darwin succeeded in convincing the world of the occurrence of evolution and ... he found (in natural selection) the mechanism that is responsible for evolutionary change and adaptation.

It is not nearly so widely recognized that Darwin failed to solve the problem indicated by the title of his work. Although he demonstrated the modification of species in the time dimension, he never seriously attempted a rigorous analysis of the problem of the multiplication of species, the splitting of one species into two. I have examined the reasons for this failure (Mayr 1959a) and found that among them Darwin's lack of understanding of the nature of species was foremost."

Mayr, 1963. Animal Species and Evolution, p. 12

3

p. 128: "By far the most frequent cause of hybridization in animals is the breakdown of habitat barriers, mostly as a result of human interference".

"Successful hybridization is indeed a rare phenomenon among animals".

Similarly, Mayr belittled local ecological races. According to Mayr, they were either separately evolved (in allopatry), or merely due to phenotypic plasticity of morphology.

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From: James Mallet jmallet@oeb.harvard.edu
To: Chris Jiggins c.jiggins@zoo.cam.ac.uk, Patrik Nosil p.nosil@sheffield.ac.uk
Subject: The Speciation Continuum
Date: 2 May 2013 16:36

I was astonished to learn today that I'm speaking at a meeting called **"Speciation Continuum:"**

Hmmm, doesn't the phrase that is the title of the meeting seem familiar from somewhere? A little research was called for, with the aid of Google of course.

I think it might have been started by us. OK, this will be a bit of a biased history (Darwin himself, of course, argued for this same continuum, but his ideas about that were put on the back burner ca. 1937 onwards). It's possible I'm giving myself airs, and the term was already out there. However, in online literature at least, Google seems to suggest it is novel. ...

[If interested in the history of terms, you can read my whole email here.]

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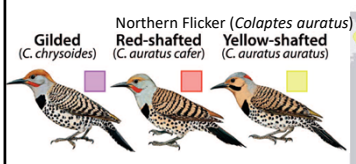
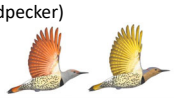
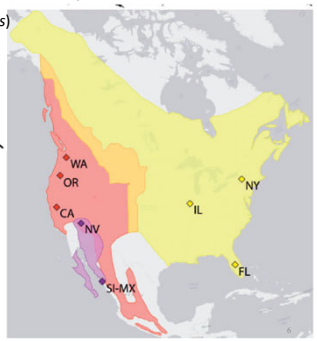
As naturalists travelled across many continents…



It began to be noticed that distinct-looking "species" varied from place to place: for example, Flickers (a genus of woodpecker)

Many hybrids
=> **subspecies**





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"The speciation continuum"

"The existence of a continuous array of sympatric biotypes—from polymorphisms, through ecological or host races with increasing reproductive isolation, to good species—can provide strong evidence for a continuous route to sympatric speciation via natural selection. Host races in plant-feeding insects, in particular, have often been used as evidence for the probability of sympatric speciation. ... Host races provide a convenient, although admittedly somewhat arbitrary intermediate stage along the **speciation continuum**."

Dres & Mallet 2002

Walsh 1867 – correspondent of Darwin "phytophagic varieties"

"Host races, as treated here, are just one of a number of intermediates in the continuum between polymorphisms and full species: other intermediate stages are often referred to as 'biotypes,' 'ecotypes,' or 'ecological races'."

Dres & Mallet 2002

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Continuum across the species boundary

- Polymorphism
- Ecological races
- Geographic races (hybrid zones)
- "Semispecies" (hybrid zones with rare hybrids)
- Hybridizing and introgressing species (later)
- "Good" species
- Higher taxa

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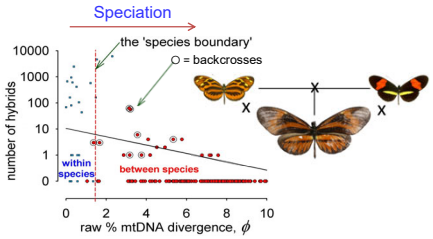
"The speciation continuum"

Natural hybrids between *Heliconius species*



Dasmahapatra et al. 2007. Biol Lett
Mallet et al. 2007. BMC Evol Biol

"Natural hybridization in heliconiine butterflies: **the species boundary as a continuum**"

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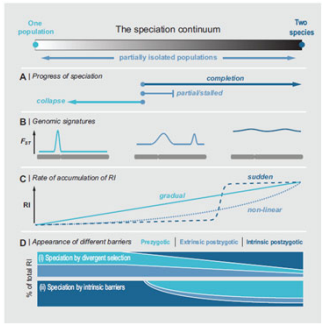
The speciation continuum

Stankowski & Ravinet pointed out that peoples' use of the term "speciation continuum" was rather loose. Variety of different meanings.

"Here, we provide an explicit definition that is compatible with the Biological Species Concept. That is, the speciation continuum is a continuum of reproductive isolation."

N.B. - $F_{ST} = \frac{\pi_B - \bar{\pi}_W}{\pi_B}$



Stankowski & Ravinet 2021

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Intermediates between species: geographic subspecies

Darwin's followers: intermediates => evolution of new species.

Systematists began to doubt whether most of these were REAL species. Instead they saw them as geographic "subspecies".

"Rassenkreise," (ring of races within a species). "Polytypic" species.

"As the new polytypic species concept began to assert itself, a certain pessimism seemed to be associated with it. It seemed as if each of the polytypic species (Rassenkreise) was as clearcut and as separated from other species by bridgeless gaps as if it had come into being by a separate act of creation. And this is exactly the conclusion drawn by men such as Kleinschmidt or Goldschmidt." Or Bateson. (Mayr 1942, p. 114)

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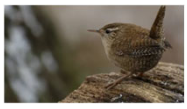
Solution to the speciation continuum

Trinominal or "Trinomial" nomenclature

By 1905 or so it was formalized by the fledgling International Commission of Zoological Nomenclature that subspecies names were allowed as a trinominal addendum to the Linnean binomial names. Thus we have: **genus – species – subspecies**

Troglodytes troglodytes troglodytes:
Common Wren (UK subspecies)



In the Northern Flicker (*Colaptes auratus*):
Colaptes auratus cafer, Red-shafted Flicker
Colaptes auratus auratus, Yellow-shafted Flicker

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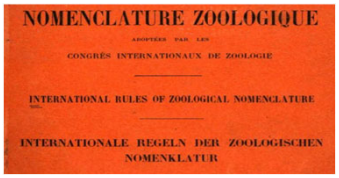
Official adoption of the subspecies in nomenclature by 1905


NOMENCLATURE ZOOLOGIQUE

ADOPTÉES PAR LES

CONGRÈS INTERNATIONAUX DE ZOOLOGIE

INTERNATIONAL RULES OF ZOOLOGICAL NOMENCLATURE

INTERNATIONALE REGELN DER ZOOLOGISCHEN NOMENKLATUR

ART. 2. — The scientific designation of animals is uninominal for subgenera and all higher groups, binominal for species, and trinominal for subspecies.

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Elliott Ladd Coues - David Starr Jordan

Elliott Coues
1884: US Bird list with trinomials
At first rejected by British systematists

David Starr Jordan
Vertebrate taxonomist
Supported idea of subspecies

Professor of Zoology, Indiana University, Bloomington
7th President Indiana University, Bloomington
1st President Stanford Univ.,
Advocacy of liberal arts
Prominent eugenicist

"Where two closely allied forms are not found to intergrade they are called distinct species. If we find actual intergradation, the occurrence of specimens intermediate in structure, the term subspecies is used"

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Natural history museum, Tring, in Hertfordshire

Curators: two Germans:
Ernst Hartert - birds
Karl Jordan - butterflies and moths

Idea of geographic subspecies

Walter Rothschild

Leading British banker
Jewish
Balfour Declaration - 1917
Foreign Secretary Arthur Balfour to Lord Rothschild, promised help for Jewish settlers in Palestine

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Walter Rothschild

Both curators, Hartert and K. Jordan, were German
Collectors from around the world
Enormous collections of birds and butterflies & moths (& fleas)
The biggest collections in the world at that time
Rothschild hired young Ernst Mayr from Berlin for New Guinea collecting – Mayr's only field trip

Lord Walter Rothschild blackmailed by "smiling peeress"
To pay, Rothschild sold bird collection to American Museum of Natural History, New York

Departure from Tring

Arrival at AMNH, New York


Doctor Mayr (right) with his Malay mantri: Arriving at Kofo, Anggi Lakes, after two months in the wild interior of New Guinea

Mayr 1932 Natural History Mag.

Mayr in 1931 moved to NY to curate this collection!
At AMNH till 1953 then Harvard
Supported trinomialism

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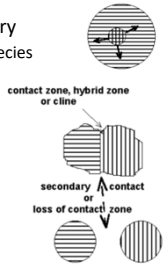
"Dimensionality" of Biological Species Concept

(According to Mayr)

- "Nondimensional:" in sympatry
  - usually clear delimitation of species
- "Multidimensional:" species include multiple allopatric or parapatric subspecies
  - often unclear delimitation



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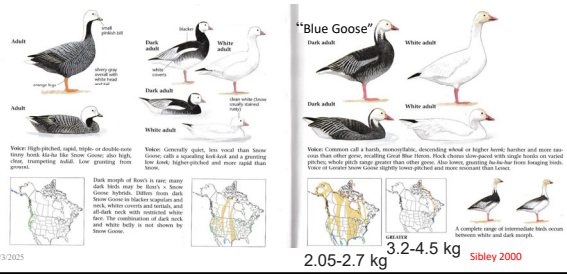
Snow Goose and relatives

Chen species

Emperor Goose
Chen canagica

Ross' Goose
Chen rossi

Snow goose
Chen caerulescens



2.05-2.7 kg
3.2-4.5 kg
Sibley 2000

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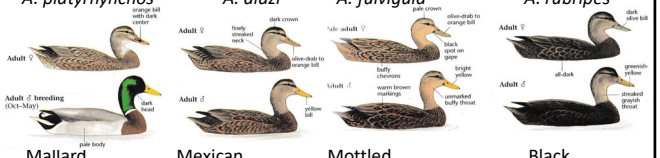
Mallard Ducks and close relatives

Anas species

A. platyrhynchos | *A. diazi* | *A. fulvigula* | *A. rubripes*



Mallard | Mexican | Mottled | Black

Sibley 2000

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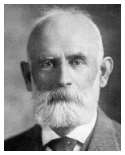
Vermivora warblers

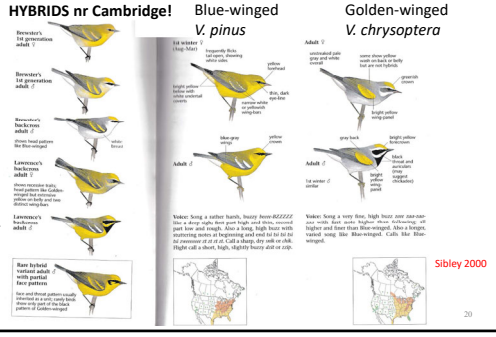


William Brewster
1851-1919
Ornithology at Harvard
Discovered "Brewster's Warbler." He later realized it was a hybrid. Bateson used these as examples of Mendelian inheritance between species

HYBRIDS nr Cambridge!

Blue-winged *V. pinus*

Golden-winged *V. chrysoptera*



Sibley 2000

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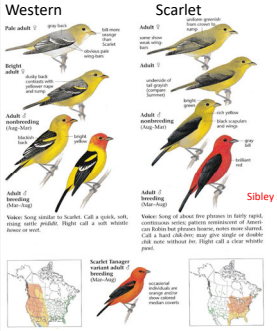
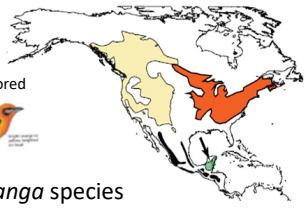
North American *Piranga* tanagers

Western | Scarlet



Sibley 2000

Flame-colored



Piranga species

Flame-colored — *P. bidentata*

Western — *P. ludoviciana*

Scarlet — *P. olivacea*

Hybrid

Manthey et al. 2016

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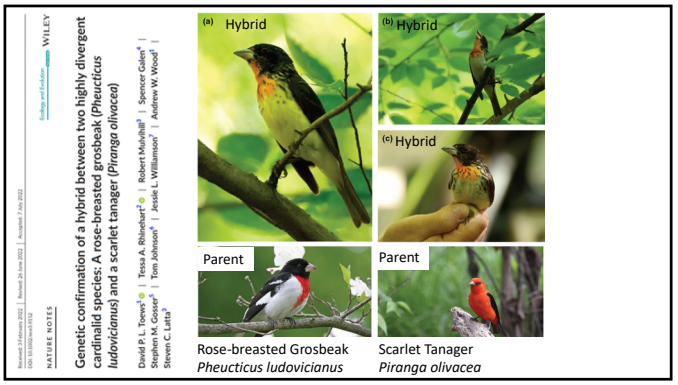

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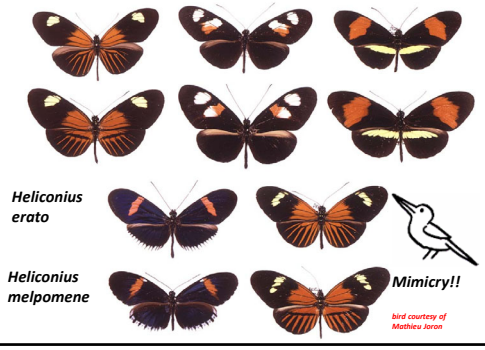
Geographic races of *Heliconius erato* and *H. melpomene*



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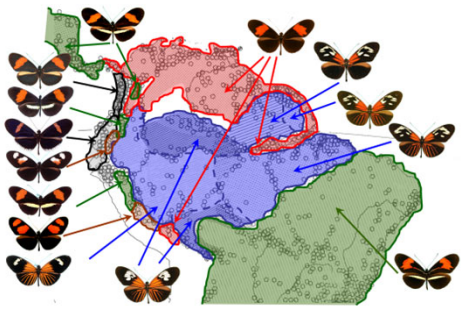
Heliconius erato mimicry races



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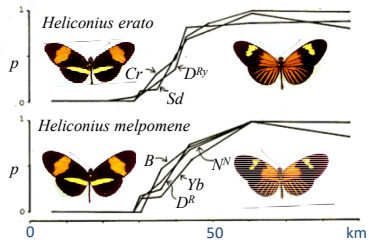
Hybrid zones between “subspecies”



Mimicry races hybridizing near Tarapoto, NE Peru

Mallet et al. 1990. Genetics

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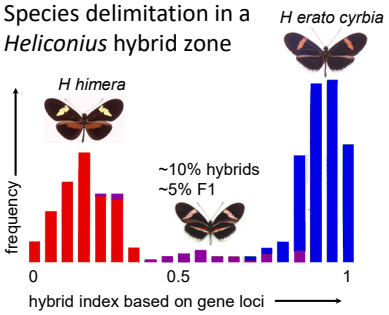
Species delimitation in a *Heliconius* hybrid zone



Jiggins et al. 1997

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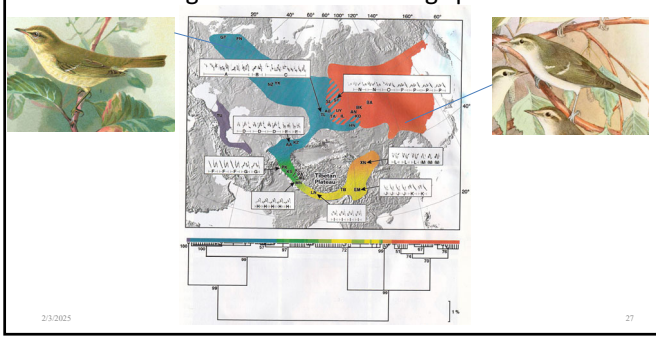
The greenish warbler “ring species”



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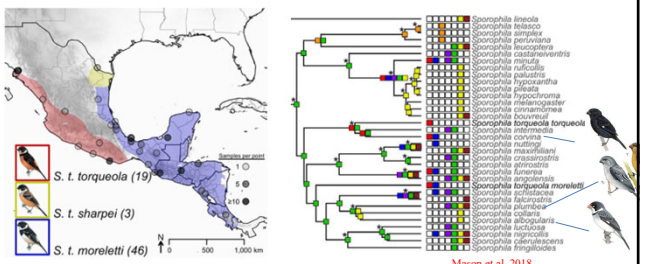
Subspecies can sometimes be wrong: White-collared Seedeater



Mason et al. 2018

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Phytophagous insect “host races”
Other types of ecological races and biotypes below the species level

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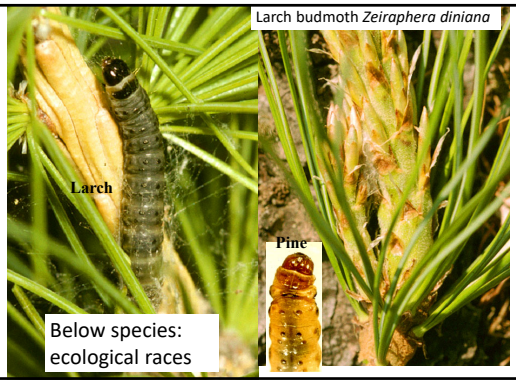

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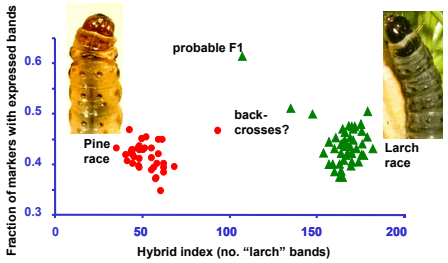
Genetic differences (AFLP) in *Zeiraphera diniana*



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

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Larch budmoth "host races":

as well as host, differ in sex attractant pheromone

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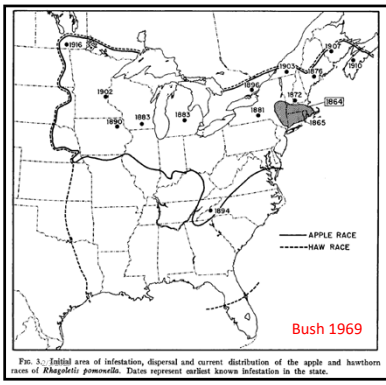
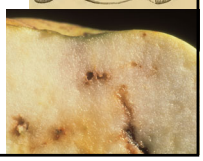


FIG. 3.—Initial area of infestation, dispersal and current distribution of the apple and hawthorn races of *Rhagoletis pomonella*. Dates represent earliest known infestation in the state.

The Apple Maggot (*Rhagoletis pomonella*)

B. Walsh 1867 – correspondent of Darwin's: "phytophagic varieties"



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

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 ≈ 0.06 per generation
3. Races do not differ in survival (apple always worst host, lower growth rate)
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
6. Apple race flies earlier than hawthorn race. *Pleiotropy* again (*allochrony*)

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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 West and Central Africa, hunter gatherers, and "Bantu speaker" peoples living in the same areas

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Crossbill ecotypes (*Loxia curvirostra* complex)

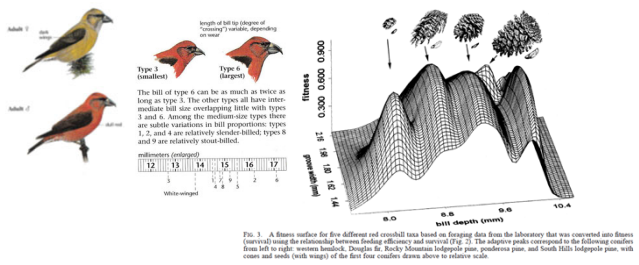

FIG. 3. A fitness surface for five different red crossbill taxa based on foraging data from the laboratory that was converted into fitness (survival) using the relationship between feeding efficiency and survival (Fig. 2). The adaptive peaks correspond to the following conifers from left to right: western 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.

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

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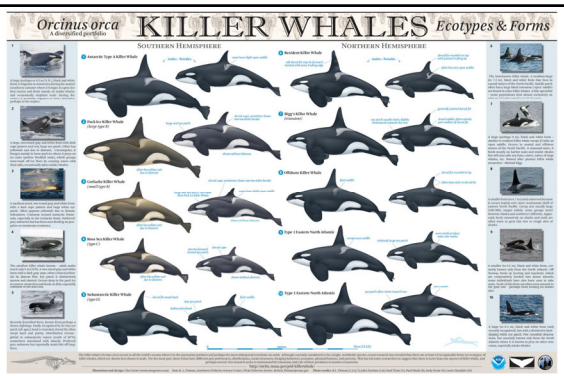

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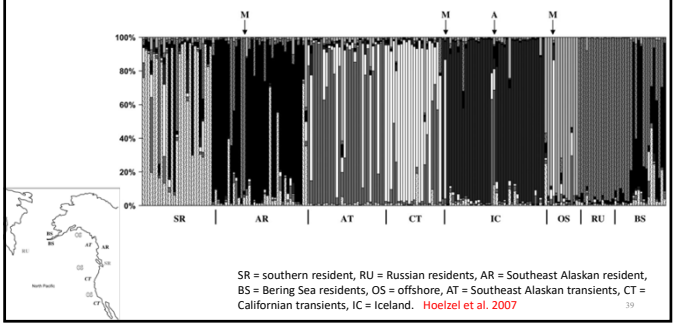
Orca population structure in the N. Pacific



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

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Mayr 1942 view on ecological races: very scanty evidence

Our discussion of ecological and biological races, of sibling and cosmopolitan species, and of so-called explosive speciation has revealed that bona fide evidence for sympatric speciation is very scanty indeed. Even if it should become evident that sympatric speciation through ecological specialization is largely nonexistent, we need not feel disturbed. The fact that geographic races can acquire considerable ecological differences, as we have seen in Chapter III (pp. 53-59), facilitates the explanation of strong biological differences between closely related species, without any recourse to a hypothetical process of sympatric speciation.

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So species unclear both from below (‘races’) And from above (hybridization)

Mayr brushed all this under the carpet…

But Darwin was maybe right all along

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