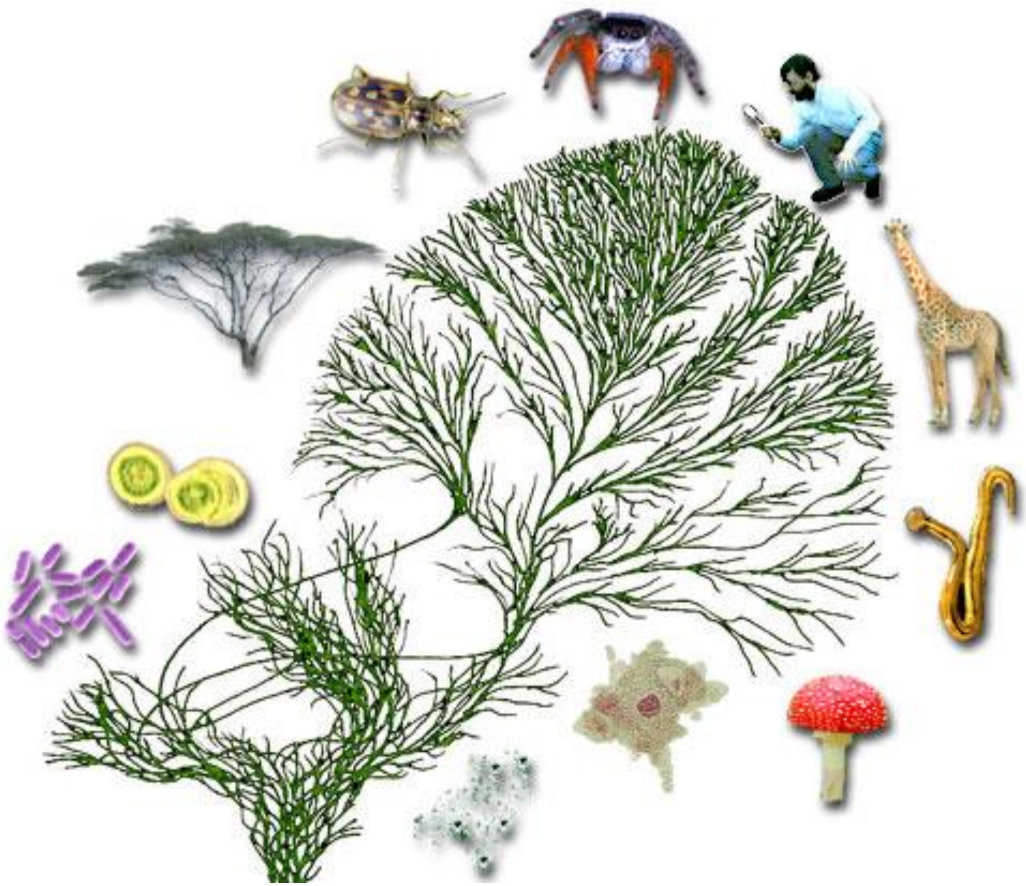
Concepts of species and the origin of species

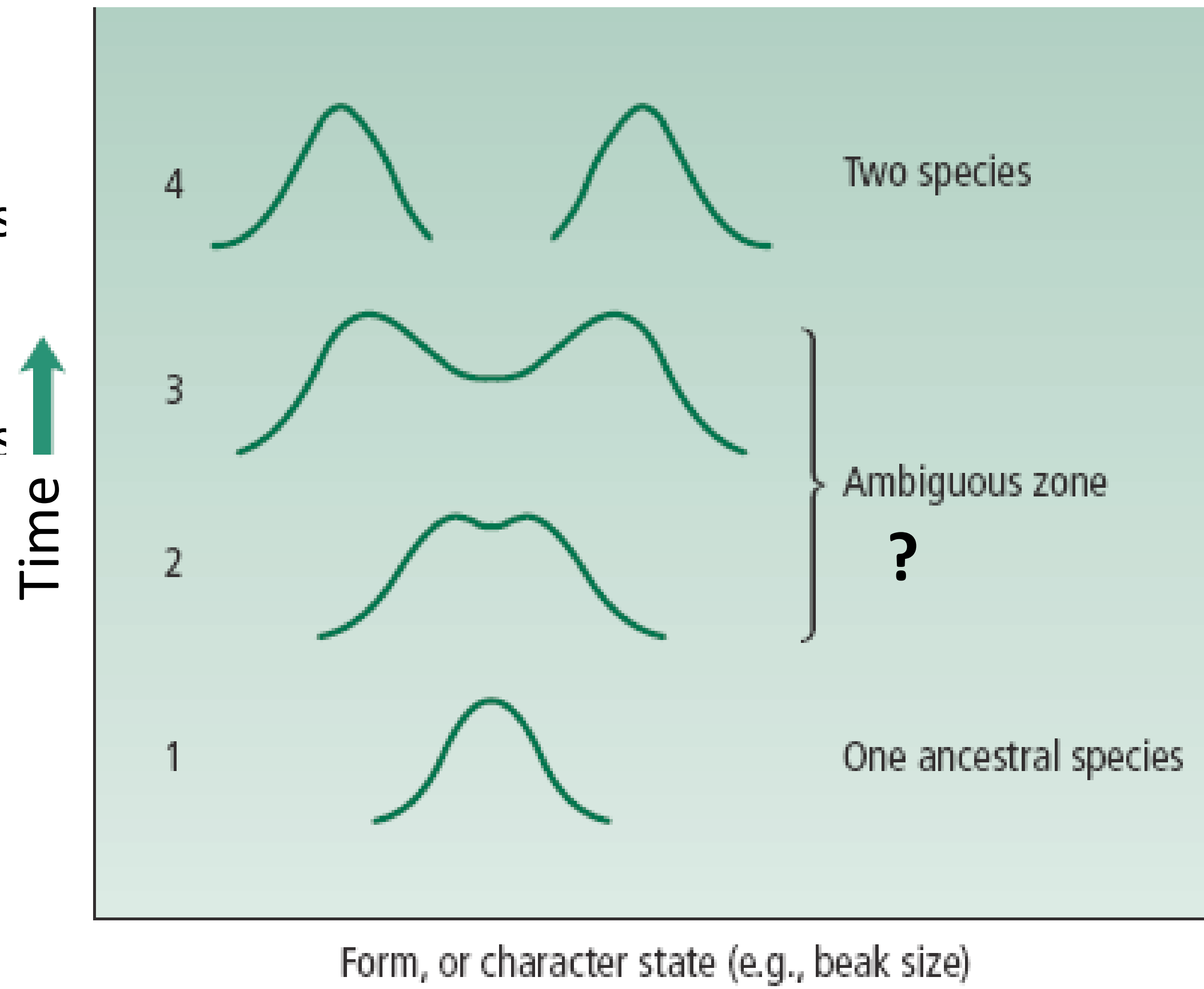


The problem of species

- Locally simple

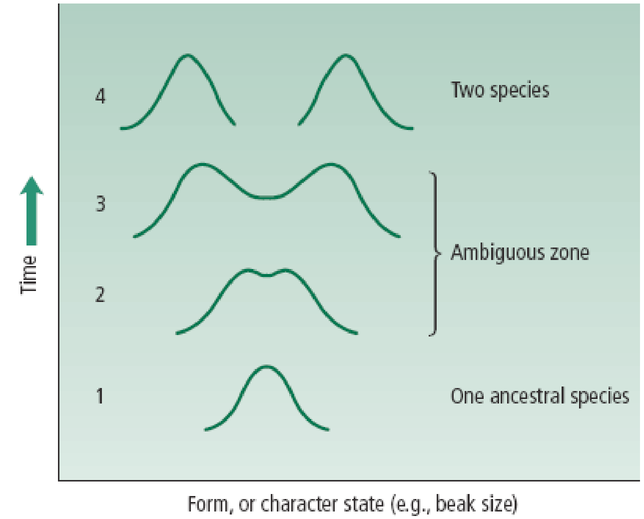
- The problem of speices arises within the whole distribution zone and in case of all related species

- The evolutionary continuity makes species hard to define



Distritubion of the character state within the population

In the formal taxonomy the species are known by their phenetic characteristics



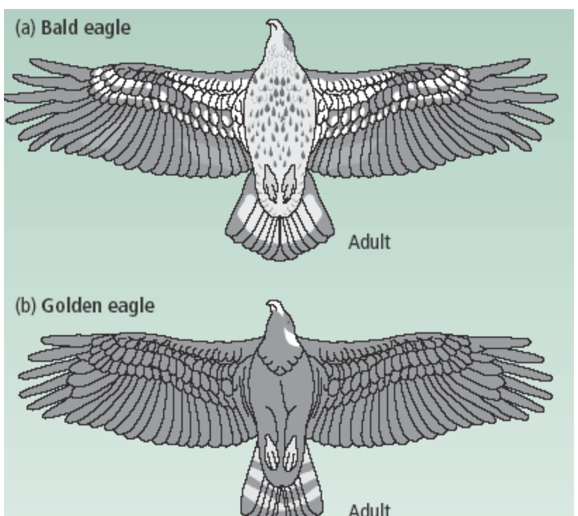
In practice by a characteristic that is unique enough

- Separates from other closeley related species

- all members of the species have it

- those characteristics are rather diagnostic than formally defining

- main problem: variety



--> when one individual does not have or has a changed diagnostic characteristic, is it a new species?

Rather a sign that this is not the way to define a species

“Ring species”

Salamanders *Ensatina eschscholtzii ssp*. Are spread to California from north, the populations devided into two and spread to both sides of San Joaquin valley. On both sides of the valley there are the subspecies with morphological and gentical differences, but they interbreed. In the South, in San Diego, the subspecies do not interbreed, there is strong selection against the F1 hybrids.

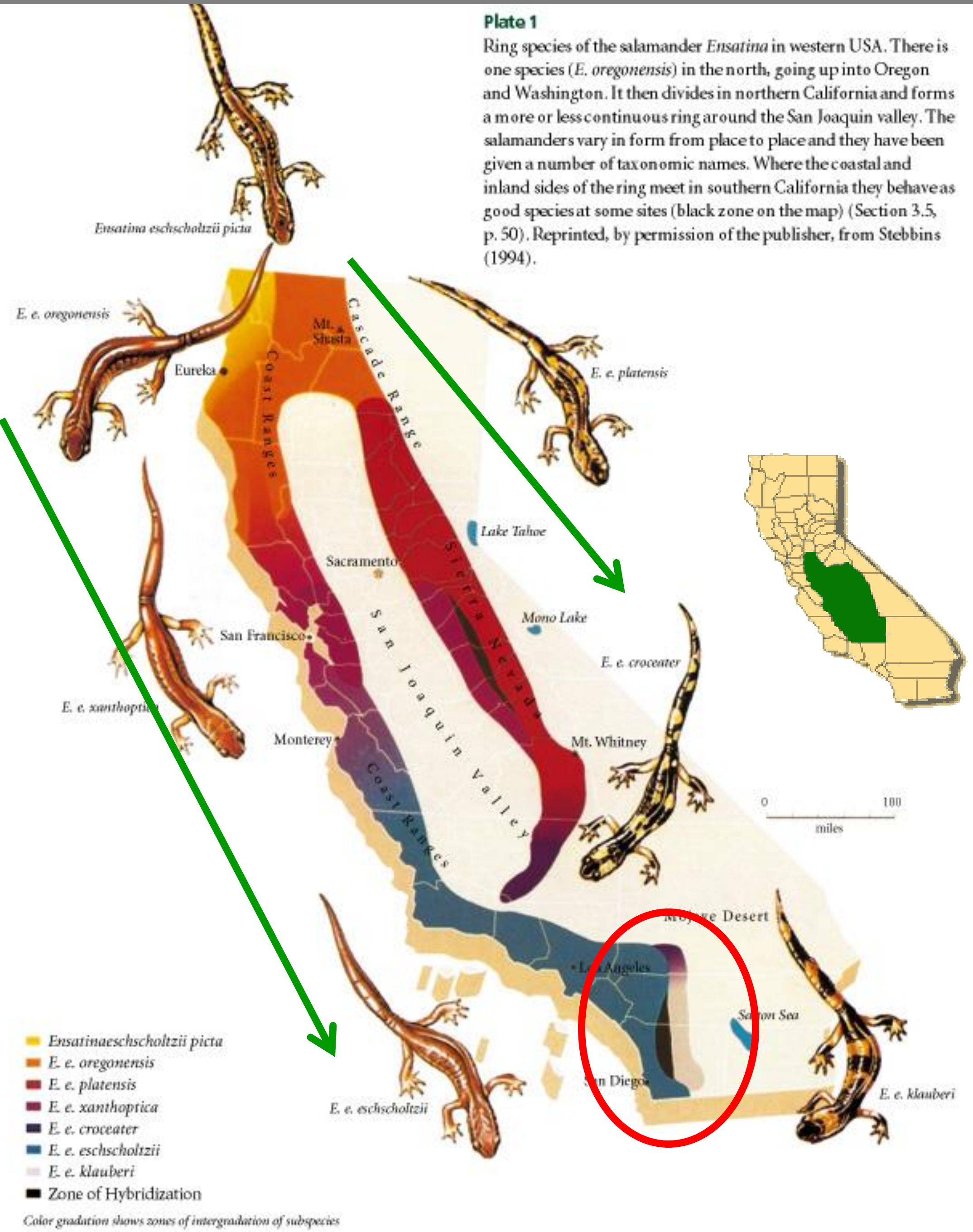


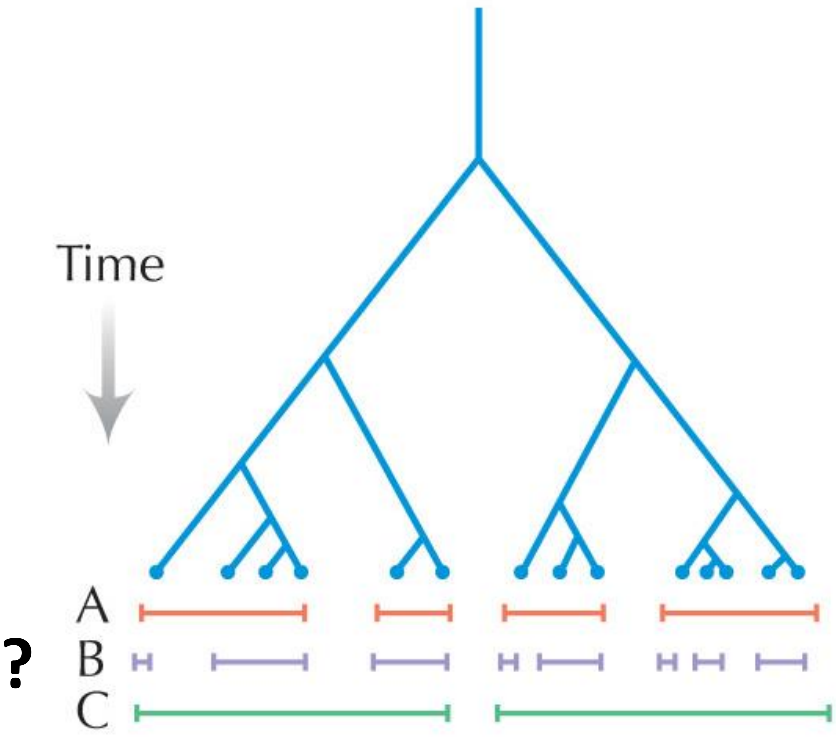
Plate 1
Ring species of the salamander *Ensatina* in western USA. There is one species (*E. oregonensis*) in the north, going up into Oregon and Washington. It then divides in northern California and forms a more or less continuous ring around the San Joaquin valley. The salamanders vary in form from place to place and they have been given a number of taxonomic names. Where the coastal and inland sides of the ring meet in southern California they behave as good species at some sites (black zone on the map) (Section 3.5, p. 50). Reprinted, by permission of the publisher, from Stebbins (1994).

The problem of species

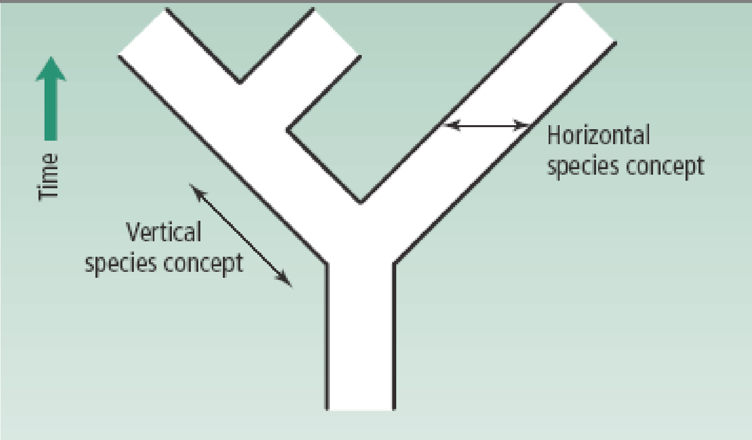
Based solely on the phylogenetic reconstruction it is hard to tell when one species became two (and it depends how we define species)

- There is no connection between the time depth of the split (the amount of molecular differences) and origin of species (at least according to the biological species concept)

- Species with the recombining DNA have a different phylogenetic tree for each locus



Concepts of species: vertical and horizontal



First one has to define what is a species?

Concepts of species

Species are defined in the given time (**horizontally**)

Concepts:

- phenetic
- reproductive (biologic)
- stressing the ecologic adaption
- cohesional (species with some uniting characteristics)

... Or through their evolutionary history (vertically)

- phylogenetic/evolutionary concepts

Concepts of species: explaining and describing

The phenetic concept of species does not explain the genesis of clusters nor the mechanisms holding them together thus is just **descriptive.**

Other major concepts of species

-biologic, ecologic, cohesional and phylogenetic are based on the mechanisms that would explain what keeps phenetic clusters together and thus are **explanatory**.

Phenetic concept of species

Morphological /

Typological /

Phenetic

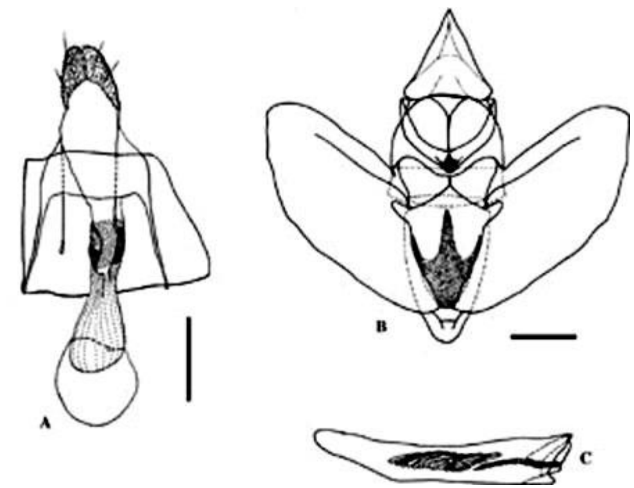
Concept of species

- **Phenetic similarity (distances)**

Phenetic concept of species

Typologic concept

Type (standard) – deviations from the type



Works well in the case of genitals of the insects (key and lock)

Carolina parakeet Museum of Zoology, University of Michigan

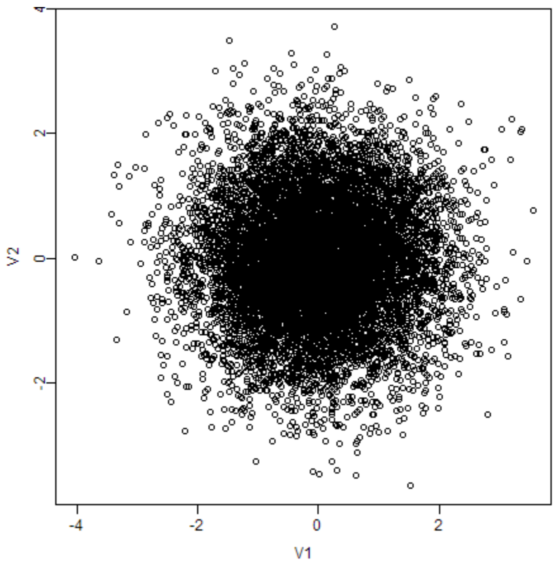
The last wild specimen was killed in Okeechobee County, Florida in 1904. The last overall died in Cincinatty zoo in 1918

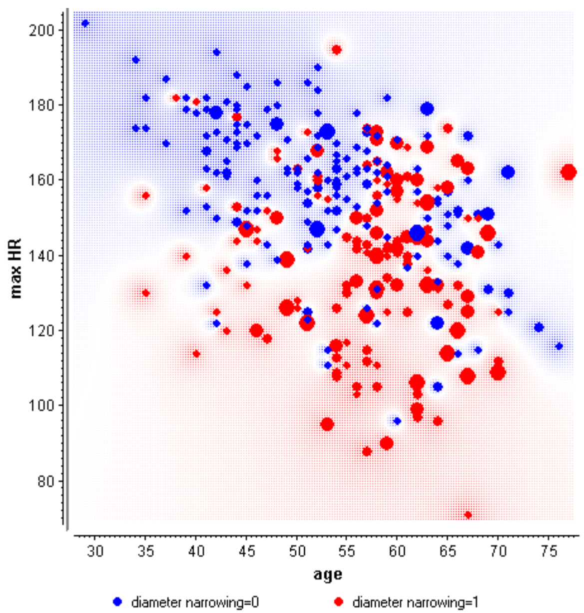
Phenetic (numerical) (1960’) concept

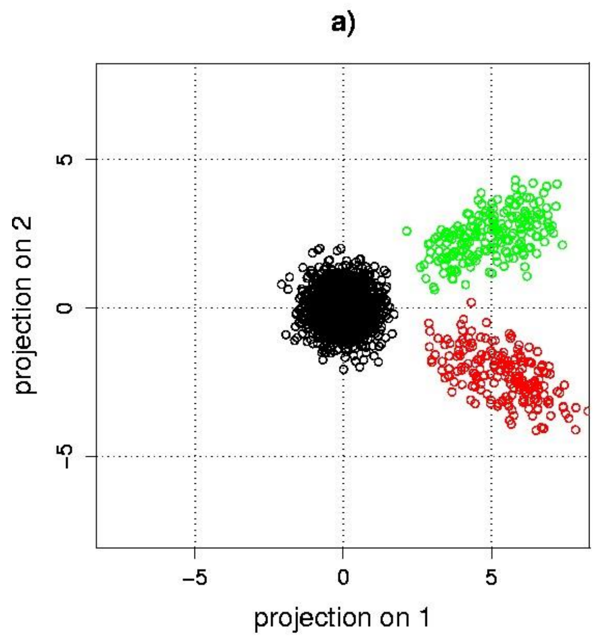
Statistics, mean values

Problems – variability (incl overlaping)

sexual dimorphism







Phenetic concept of species

Despite of the criticism the concept works on a general level: Mayr visited New Guinea in 1920s where local aboriginal people (Arfaks) knew 136 bird species of which 135 are considered species also today, based on different criteria.

Reason: phenetic clusters arose because of genetic similarity of the interbreeding individuals.

Phenetic concept of species

Everery individual on the picture represents a separate biological species

(e.g. Müller’s mimicry)

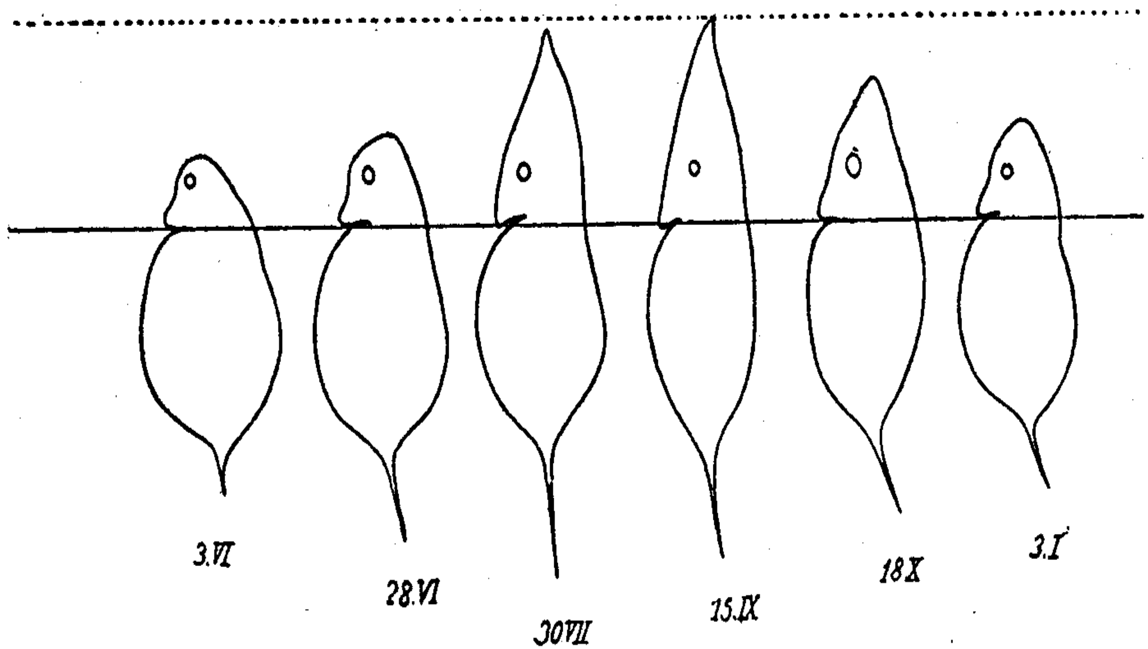
Phenetic concept of species

Spiders *Theridion grallator*. All are from one biologic species, they interbreed

Phenetic concept of species

Phenotypic plasticisity

Water flea (*daphnia*)

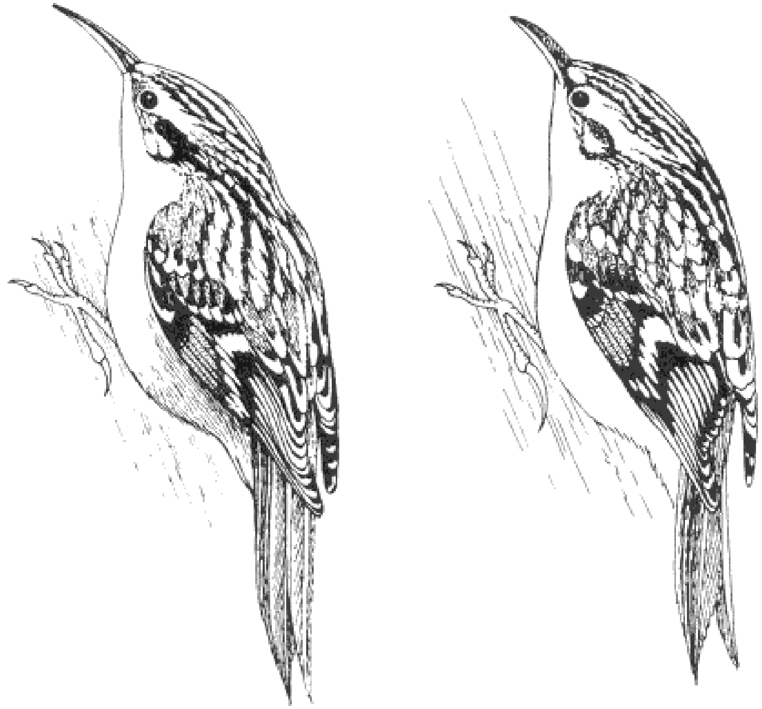


Woltereck (1909): “helmet” formation as response to predators, chemically stimulated

Schmalhausen (1949) *Reaktionsnorm* (Reaction norm)

Phenetic concept of species

Sister species are problematic – phenotypically similar but not interbreeding



C. brachydactyla & C. familiaris

Treecreepers (*Certhia*)

Researcher of phenetic concepts has less trouble when dealing with local species – less plausible to collide into allopatric sisterlineages

Biolological species concept

John Ray 1660s:
"you belong with organisms that you interbreed with"
Dobzhansky 1937
Ernst Mayr 1942:
"A biological species is defined as a population or group of populations whose members have the potential to interbreed and produce viable, fertile offspring but cannot do so with members of other species

Ernst Mayr 1969: "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups."
Ernst Mayr 1982: A species is a reproductive community of populations (reproductively isolated from each other) that occupies a specific niche in nature."

Biolological species concept

- Species are groups of populations in nature that are freely interbreeding with each other and reproductively isolated from other such groups

A community of interbreeding organisms make up, in population genetic terms, a **gene pool**. In theory, the gene pool is **the unit within which gene frequencies can change**. In the biological species concept, gene pools become more or less identifiable as species.

- interbreeding in artificial conditions does not count
- Geogrpahic barrers do not count, e.g many canine species do not excist ac cording to this

– Phylogenetic tree of organelles' DNA *vs* autosomal DNA or adaptions – cross-species hybrids

+ Evolutionary argumented explanation

Biolological species concept

According to biological species concept the species is held together as a cluster by:

- **<u>Gene flow</u>**

- **<u>Epistatic</u> relations**

Selection favours genes that work well together with other genes from that organism

Cohesional species concept

Cohesional concept of species suits also for asexual species

According to this the individuals are kept together as a discrete phenotypic unit by some mechanism – restricted geneflow (barrier to interbreeding); stabilizing selection (adaption to a niche); historical, developmental or ecological restrictions.

Ecological concept of species

"Species is a group of organisms who uses or is adapted to the same ecological niche"

Orgranisms appear as phenetic clusters due to ecological and evolutionary processes that define the <u>use of resources.</u>

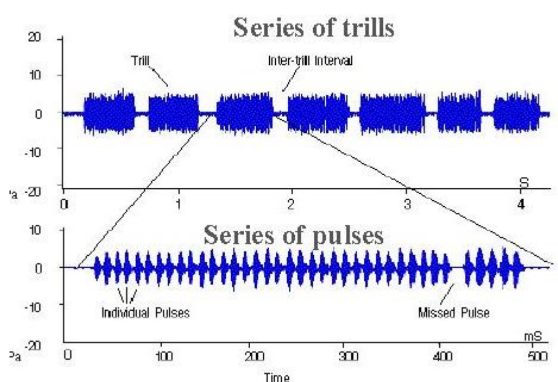
E.g. a new species of parasites arises when they adapt to the new host organism. When two species of parasites would interbreed their progeny would be adapted to an intermediate non-existant host/niche.

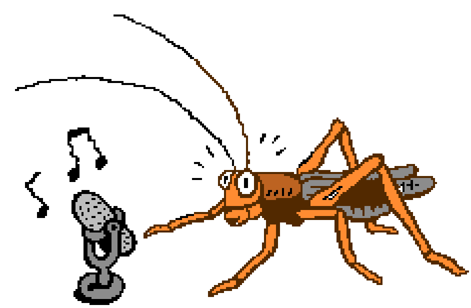
Recognition species concept

Recognition species concept is also biological concept:

•A species is comprised of those who share caracteristics in recognition of the partner.
•Stresses similarity and recognition, differences and inaptitudes are the result of not recognising

In America there are 30-40 cricket species living together, the females distinguish their species by the sound of the males.

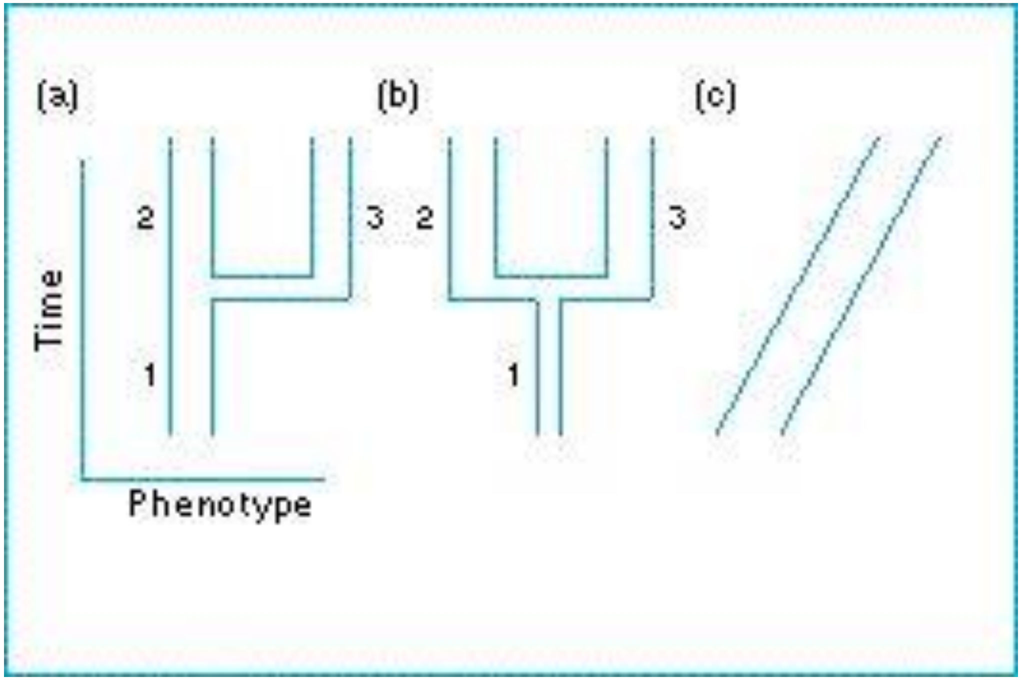




Phylogenetic species concept (Vertical!)

Cladistic species concept

Species are reproductively isolated natural populations or groups of populations. Species arise from a parental species during the emergence of species and disappear during extinction or emergence of new species.



+ congruent with phylogeny

- The extinction of parental species during emergence of species (a)

Has not much practical values because there is not enough data about phylogeny

Evolutionary concept of species

Evolutionary concept of species has been harnessed in cases of fossils

Population line in the parent-offspring relations that has its own identity discerning it from other lineages; and its own evolutionary path and history

Biology and genetics are less important.
Does not discuss hybridisation.

Different concepts in different cases?

Plural concept of species

Different concepts applied for different species

- every day use

- confusion

Taxons higher than species:

- Mayr (Biological concept): only speices is real
- According to the **phenetic** and **ecological concept** all other taxons higher than species are real

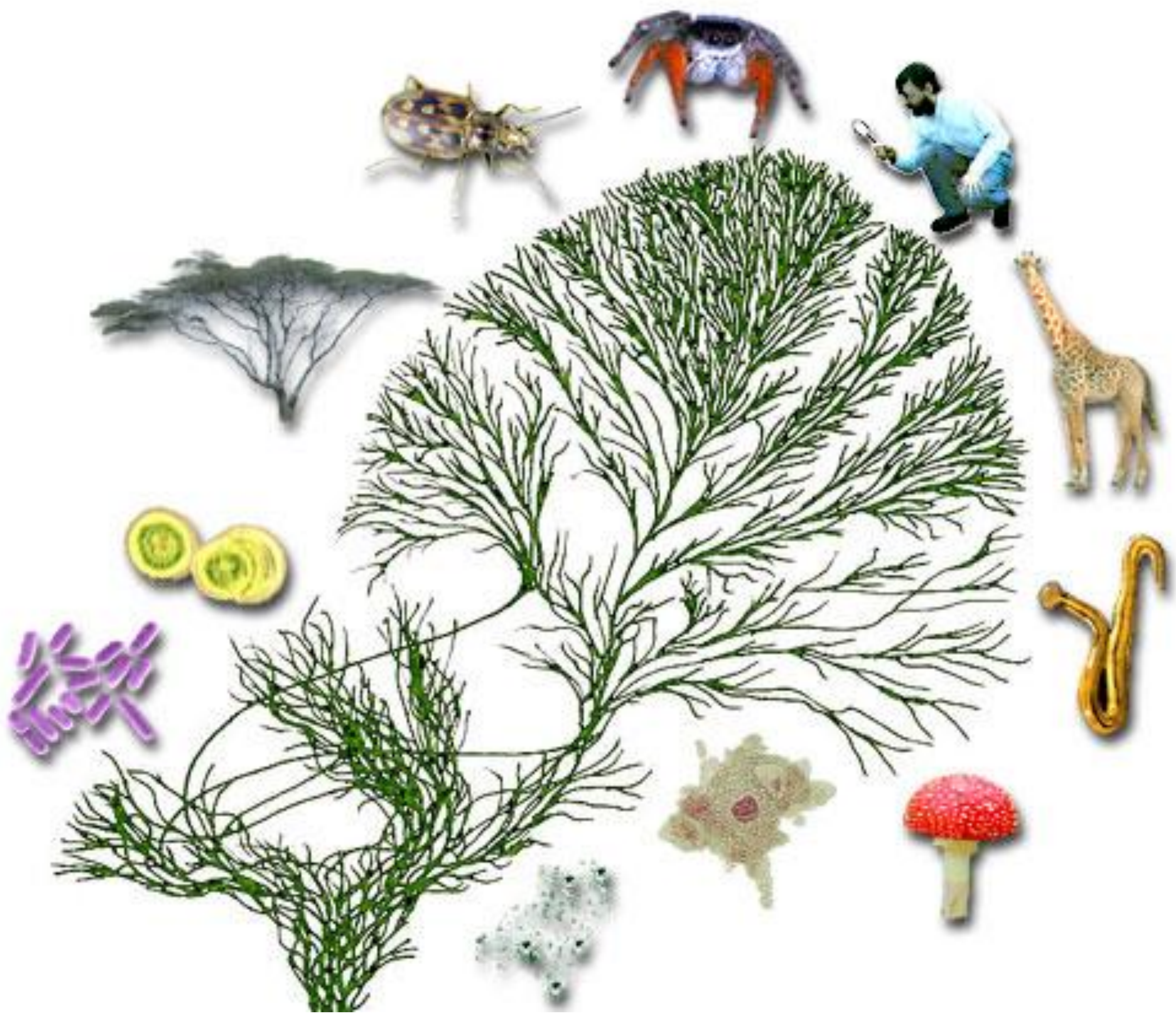
Summary

- Concepts of species – vertical and horizontal
- Concepts define species based on:
  - Phenenetic - similarity between species
  - Biological - the capacity to interbreed
  - Reconition - recognition mechanisms that guarantee interbreeding
  - Ecological - according to the adaption to ecological niches

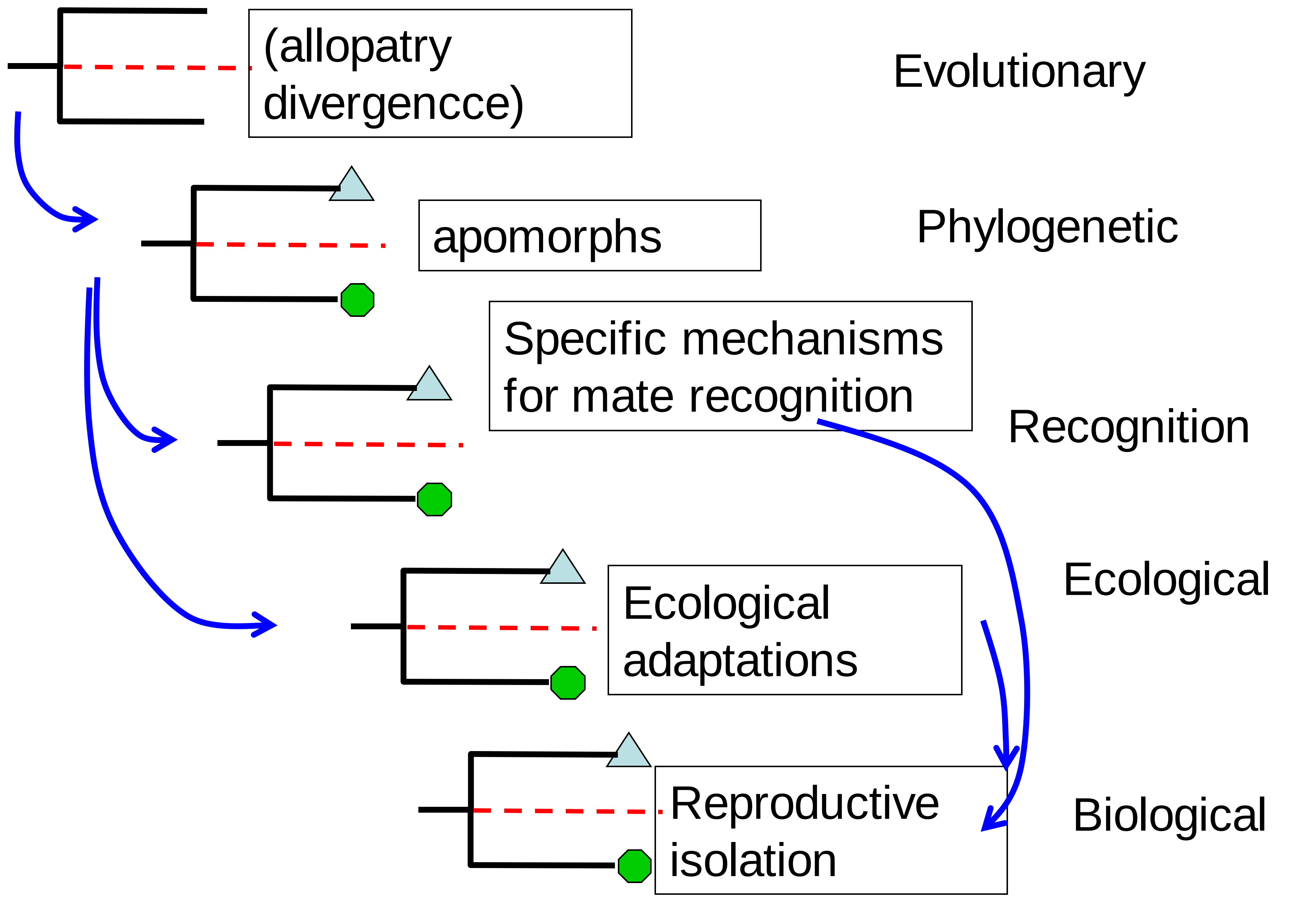
  - Biological concept explains the coherence of characteristics of a species (as the only real taxon) based gene flow and epistatic relations whereas ecologic concept does it through selection. Both processes usually work together.

  - Phylogenetic - defines species as evolutionary lines

Origin of species



Timing of the speciation event depends on the species concept you use



-In the following we shall study speciation within the BIOLOGICAL species concept.
-This is not to say taht this is the only “correct” concept but rather that genetic studies have (and can) mostly considered this aspect of speciation

Two types of reproductive isolation

prezygotic:

- Organisms don’t meet– time and space
- Mating does not occur– behaviour or say blossoming time differences
- Gametic isolation, no fertilization of the egg

postzygotic:

- Defects in the development of the hybrid embryo
- F1 hybrid is sterile
- F2 hybrid is sterile

Geographic isolation will lead to reproductive isolation

Geographic isolation will lead to reproductive isolation and we can test/confirm/observe that in

nature

and

Laboratory experiments

Geographic isolation will lead to reproductive isolation

“Ringspecies”

Cumulative gec
over long dista
reproductive is
subpopulations
can all reprodu
neighbors. All k
Diego.

Plate 1
Ring species of the salamander *Ensatina* in western USA. There is
(*E. oregonensis*) in the north, going up into Oregon
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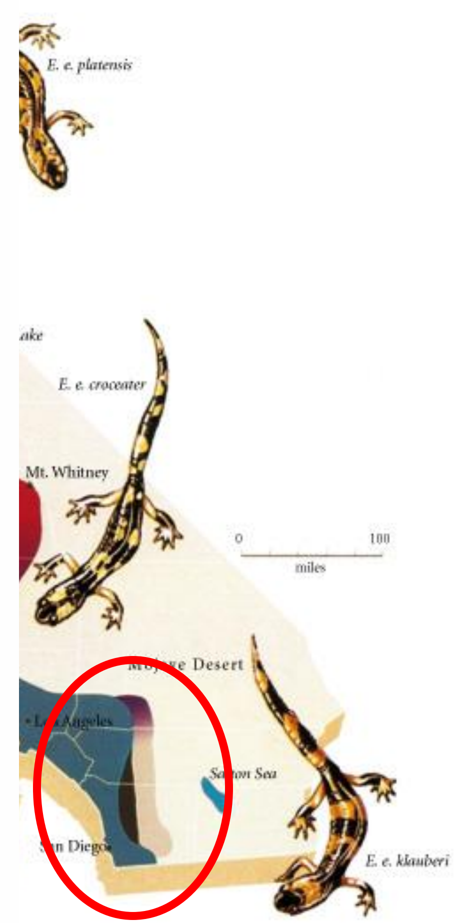
Salamandrid

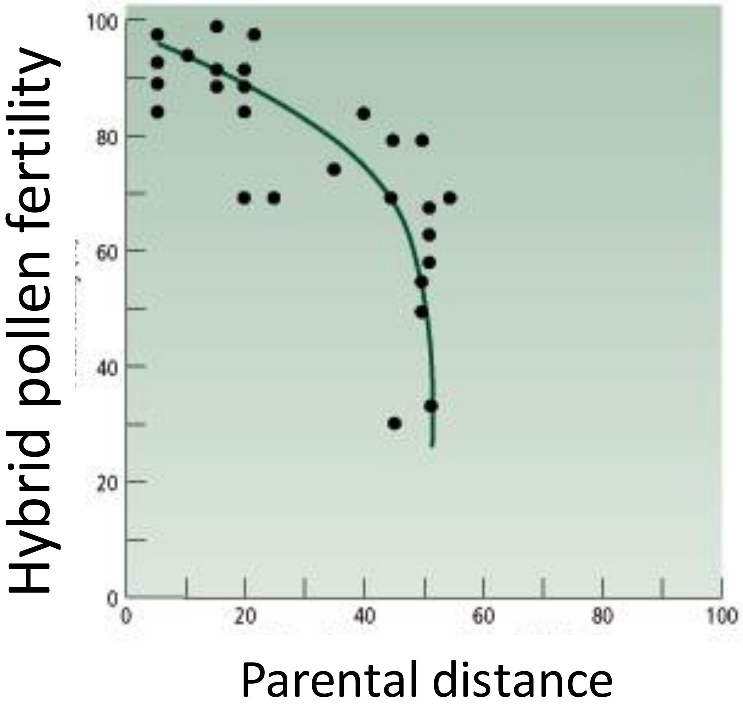
Ensatina sp.



Zone of Hybridization

Color gradation shows zones of intergradation of subspecies

Geographic isolation will lead to reproductive isolation



Jewel Flower
(Streptanthus glandulosus)

Postzygotic isolation

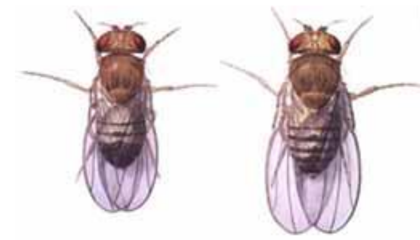
Figure 14.4
Postzygotic isolation between populations of the Californian flower *Streptanthus glandulosus*. Flowers taken from different populations were crossed, and produced hybrids. The amount of good pollen produced by the hybrid offspring was measured and expressed as a percentage of the pollen produced by the parents. Hybrids from more distant crosses tended to be less fertile. (50 miles = 80 km.) Redrawn, by permission of the publisher, from Kruckeberg (1957).

Geographic isolation will lead to reproductive isolation

PNAS | November 7, 2000 | vol. 97 | no. 23 | 12637–12642

Nonrandom mating in *Drosophila melanogaster* laboratory populations derived from closely adjacent ecologically contrasting slopes at "Evolution Canyon"

Abraham Korol*, Eugenia Rashkovetsky*, Konstantin Iliadi*, Pawel Michalak*†, Yefim Ronin*, and Eviatar Nevo*‡



Mount Carmel

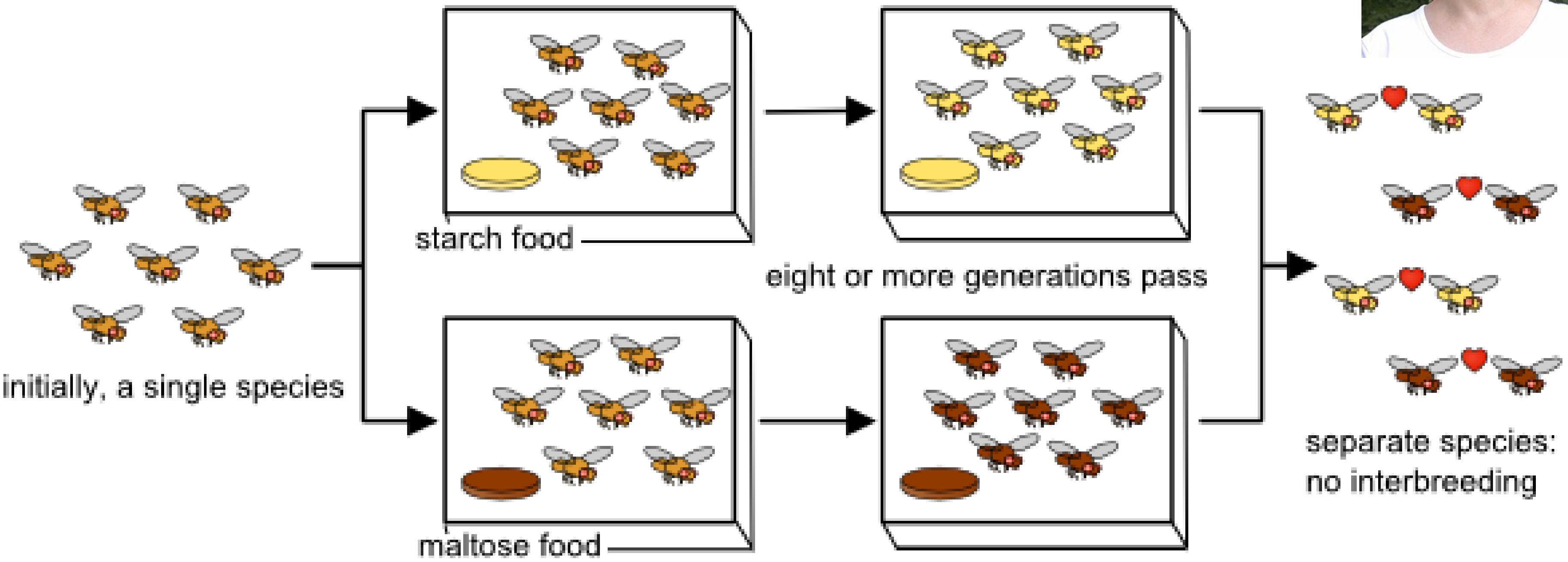
Flies from different micro-locations (micro-ecological nishes) will prefer to mate with flies from the same location.

Prezygotic isolation

Adaptive radiation will lead to reproductive isolation FASTER!

Reproductive Isolation as a Consequence of Adaptive Divergence in Drosophila pseudoobscura
Diane M. B. Dodd
Evolution, Vol. 43, No. 6 (Sep., 1989), pp. 1308-1311

Prezygotic isolation



In this experiment it was shown that 8+ generations of geographic isolation in fruit flies was not sufficient to induce prezygotic isolation. However – when the geographically isolated populations were also subject to strong natural selection – they were grown on either exclusively starch or maltose – then the two groups did also evolve to prefer flies from their own group as mates. This is an important example where adaptive radiation actively promotes speciation by inducing reproductive isolation.

Prezygotic reproductive isolation as a consequence of adaptive radiation – how can this happen?

Pleiotropy – One gene affect several phenotypes (use of recourse and mate preference)

Genetic hitchhiking– A gene responsible for mate recognition is linked to the gene under positive selection in adaptive radiation. (No good examples found yet but theoretically sound)

NATURE | VOL 409 | 11 JANUARY 2001 |

Correlated evolution of morphology and vocal signal structure in Darwin's finches

Jeffrey Podos

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA

Speciation in many animal taxa is catalysed by the evolutionary diversification of mating signals[1]. According to classical theories of speciation, mating signals diversify, in part, as an incidental byproduct of adaptation by natural selection to divergent ecologies[2,3], although empirical evidence in support of this hypothesis has been limited[4–6]. Here I show, in Darwin's finches of the Galápagos Islands, that diversification of beak morphology and body size has shaped patterns of vocal signal evolution, such that birds with large beaks and body sizes have evolved songs with comparatively low rates of syllable repetition and narrow frequency bandwidths. The converse is true for small birds. Patterns of correlated evolution among morphology and song are consistent with the hypothesis that beak morphology constrains vocal evolution, with different beak morphologies differentially limiting a bird's ability to modulate vocal tract configurations during song production. These data illustrate how morphological adaptation may drive signal evolution and reproductive isolation, and furthermore identify a possible cause for rapid speciation in Darwin's finches.

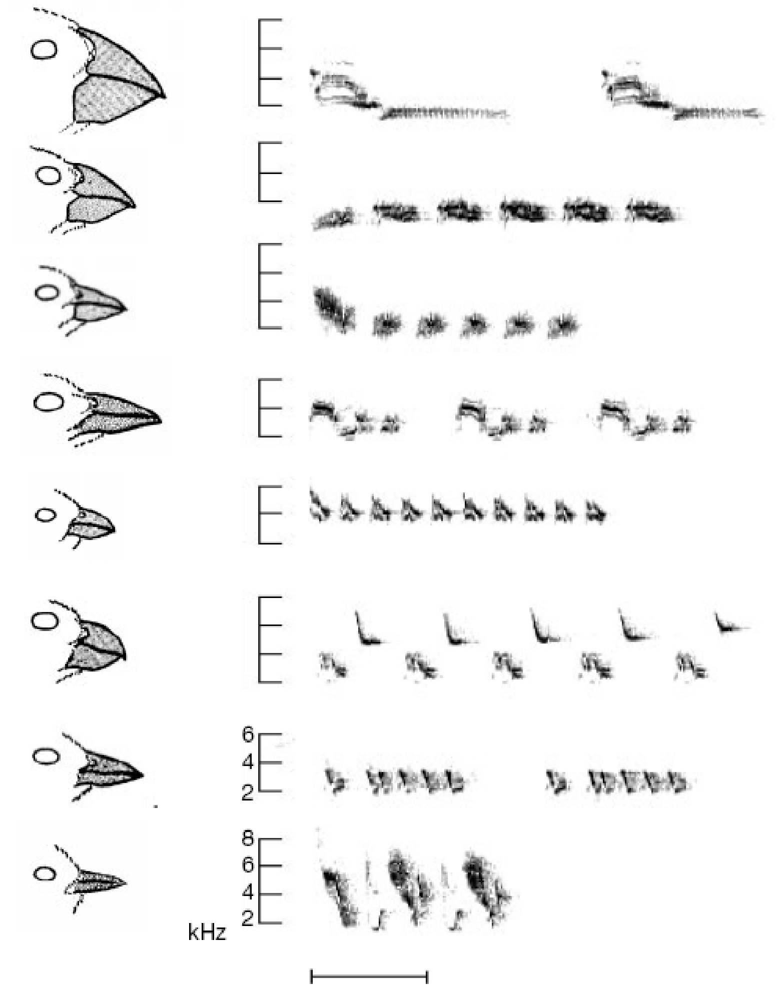


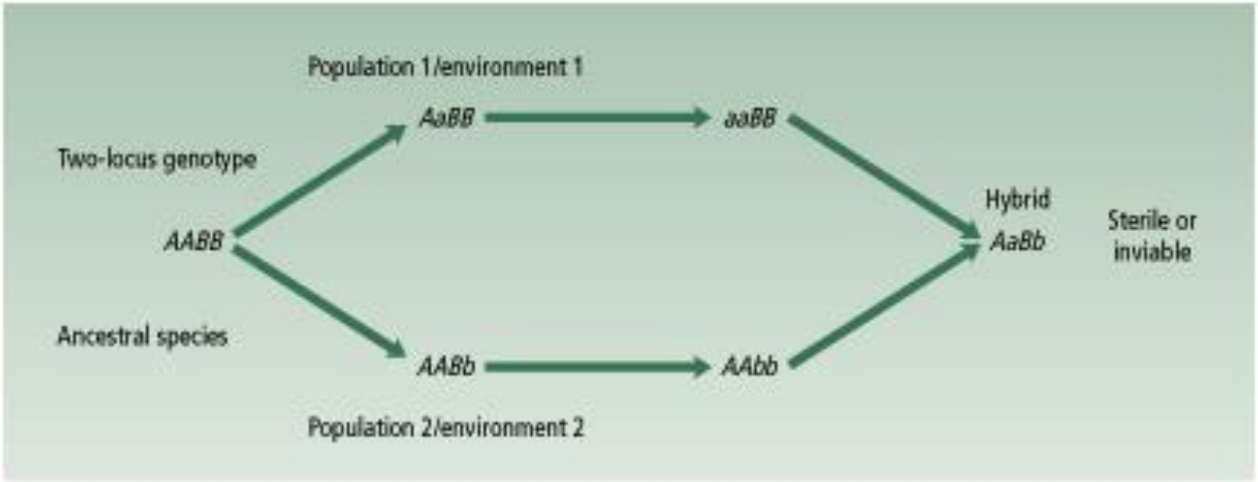
Figure 1 Beak morphology (sketches reprinted[15]) and representative sound spectrograms of songs from eight Darwin's finch species on Santa Cruz Island (from top to bottom: *G. magnirostris*, *G. fortis*, *G. fuliginosa*, *G. scandens*, *C. parvulus*, *C. psittacula*, *C. pallida*, *C. olivacea*). Interspecific variation is apparent in both morphology and song structure. Comparability of the songs of different species is supported by the young age of the clade[19], and the striking uniformity among species in the structure of the syrinx and associated musculature[22]. See ref. 16 for a discussion of homology among Darwin's finch songs. Spectrogram frequency resolution, 98 Hz; scale bar, 0.5 s.

The genetics of prezygotic reproductive isolation is less understood than that of postzygotic isolation.

The theory of **postzygotic** isolation of Dobzhansky & Müller

Figure 14.5
The Dobzhansky–Muller theory for the evolution of postzygotic isolation. An ancestral species splits into more than one population, between which gene flow is absent. Each population adapts to its local conditions by genetic change. The genetic changes are likely to be at different gene loci in the different populations. If the two populations later meet up, the genetic changes in each will probably be incompatible and the hybrids sterile or inviable. The genotypes shown are for two loci. *A* and *a* are alleles at one locus; *B* and *b* are alleles at a second locus.

…postzygotic isolation is determined by noncompatible epistatic relations of genes from several loci



OPEN ACCESS Freely available online PLoS BIOLOGY

Autoimmune Response as a Mechanism for a Dobzhansky-Muller-Type Incompatibility Syndrome in Plants

Kirsten Bomblies[1☯], Janne Lempe[1☯], Petra Epple[2], Norman Warthmann[1], Christa Lanz[1], Jeffery L. Dangl[2,3,4], Detlef Weigel[1*]

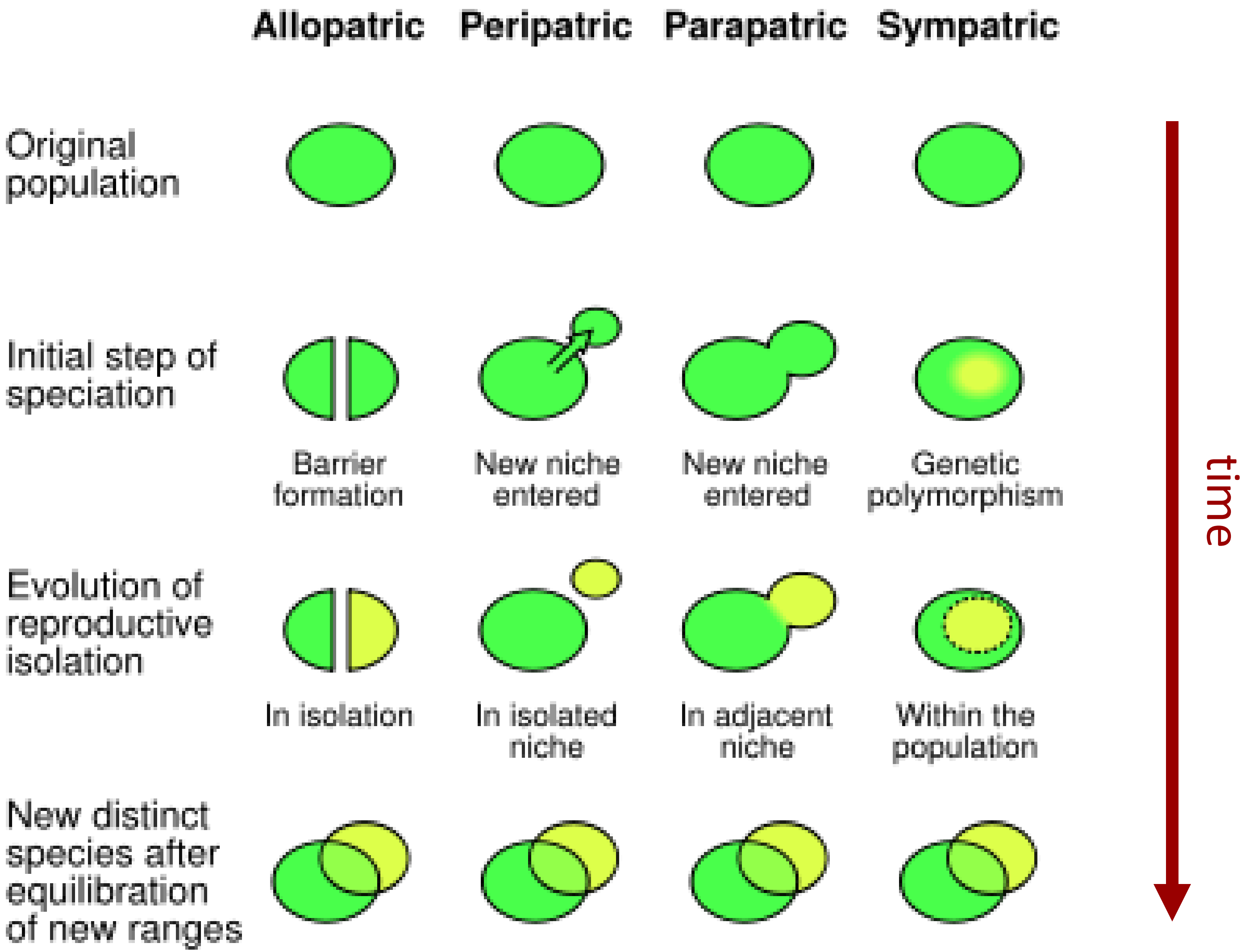
1 Max Planck Institute for Developmental Biology, Tübingen, Germany, 2 Department of Biology, University of North Carolina, Chapel Hill, North Carolina, United States of America, 3 Department of Microbiology and Immunology, University of North Carolina, Chapel Hill, North Carolina, United States of America, 4 Carolina Center for Genome Sciences, University of North Carolina, Chapel Hill, North Carolina, United States of America

Epistatic interactions between genes are a major factor in evolution. Hybrid necrosis is an example of a deleterious phenotype caused by epistatic interactions that is observed in many intra- and interspecific plant hybrids. A large number of hybrid necrosis cases share phenotypic similarities, suggesting a common underlying mechanism across a wide range of plant species. Here, we report that approximately 2% of intraspecific crosses in *Arabidopsis thaliana* yield F_1 progeny that express necrosis when grown under conditions typical of their natural habitats. We show that several independent cases result from epistatic interactions that trigger autoimmune-like responses. In at least one case, an allele of an *NB-LRR* disease resistance gene homolog is both necessary and sufficient for the induction of hybrid necrosis, when combined with a specific allele at a second locus. The *A. thaliana* cases provide insights into the molecular causes of hybrid necrosis, and serve as a model for further investigation of intra- and interspecific incompatibilities caused by a simple epistatic interaction. Moreover, our finding that plant immune-system genes are involved in hybrid necrosis suggests that selective pressures related to host–pathogen conflict might cause the evolution of gene flow barriers in plants.

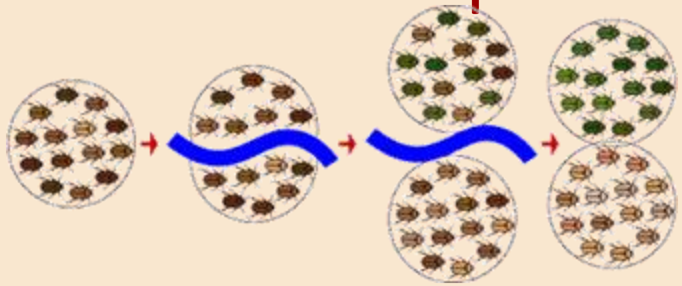
Interim summary:

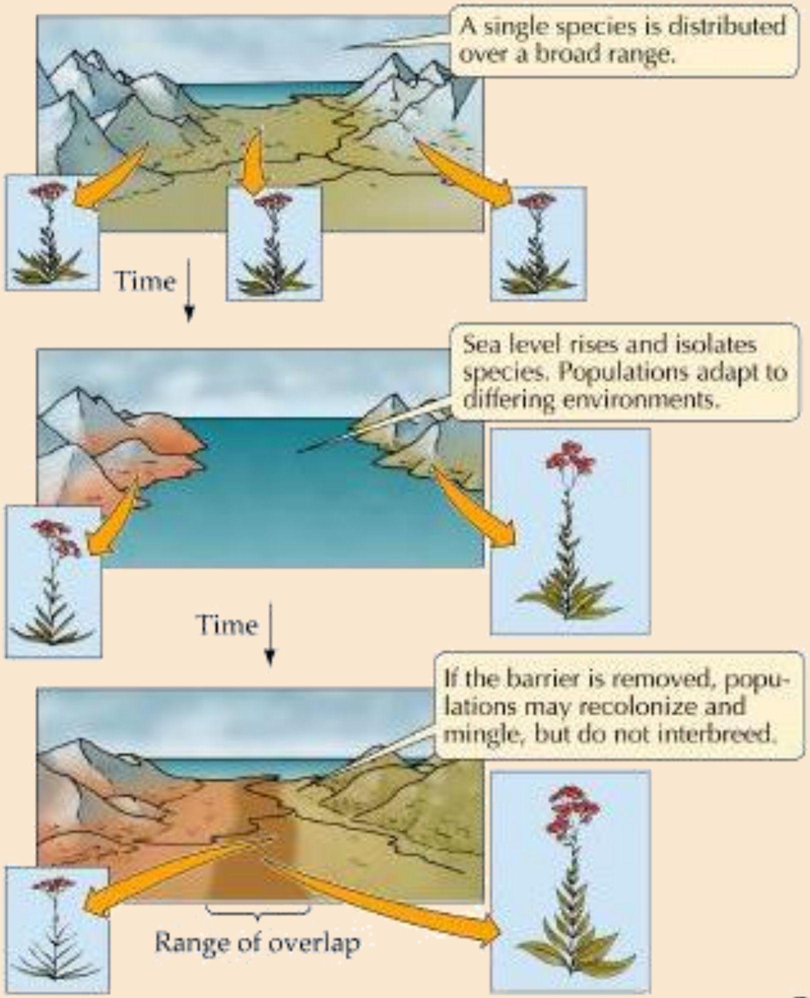
- Geographic isolation will result in reproductive isolation but the process is faster if the separated populations also adapt to different environments (adaptive radiation).
- There are a few hypotheses to explain the genetics behind prezygotic isolation but it is hard to test these.
- Postzygotic isolation develops through incompatibilities of the epistatic relations between different loci

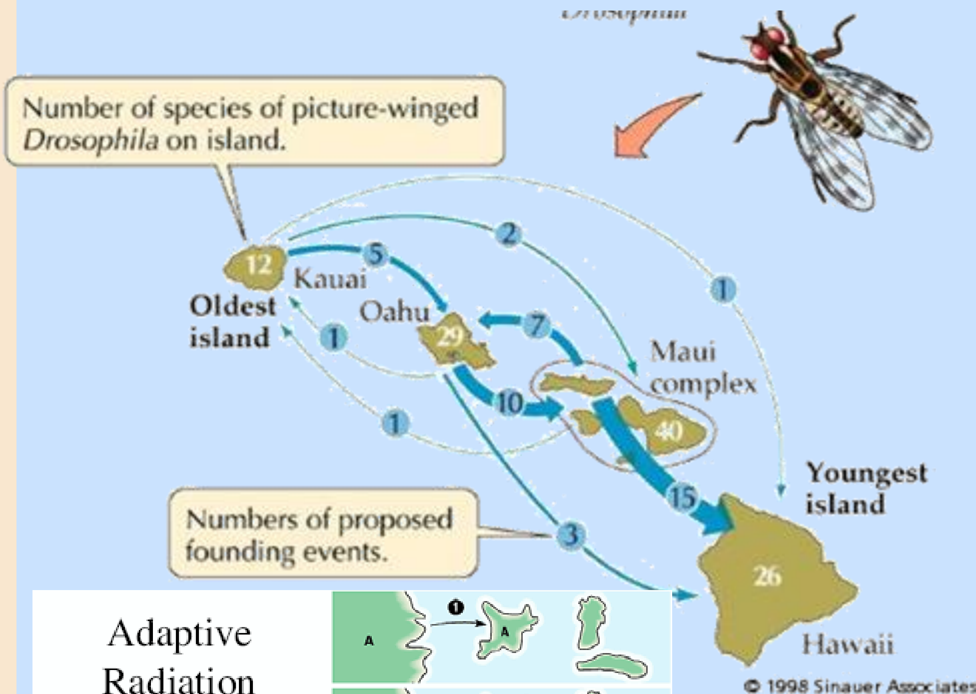
Models of speciation



vicariance Allopatric Peripatric (colonizing event)

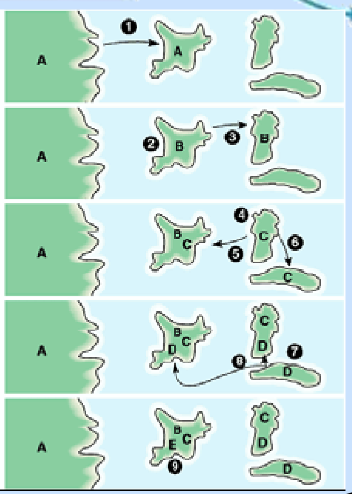


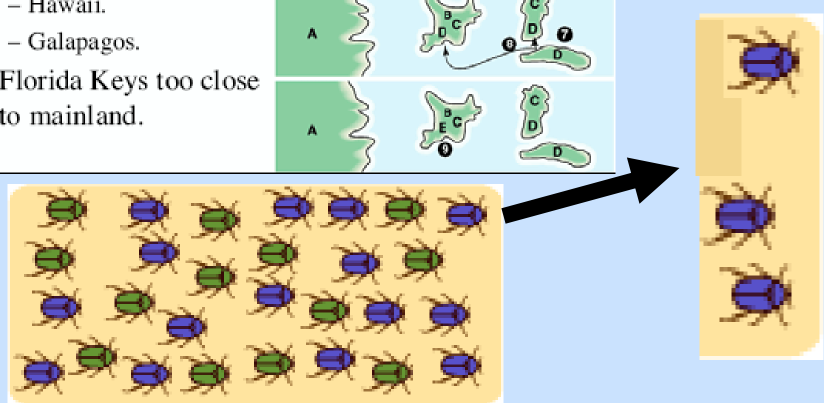




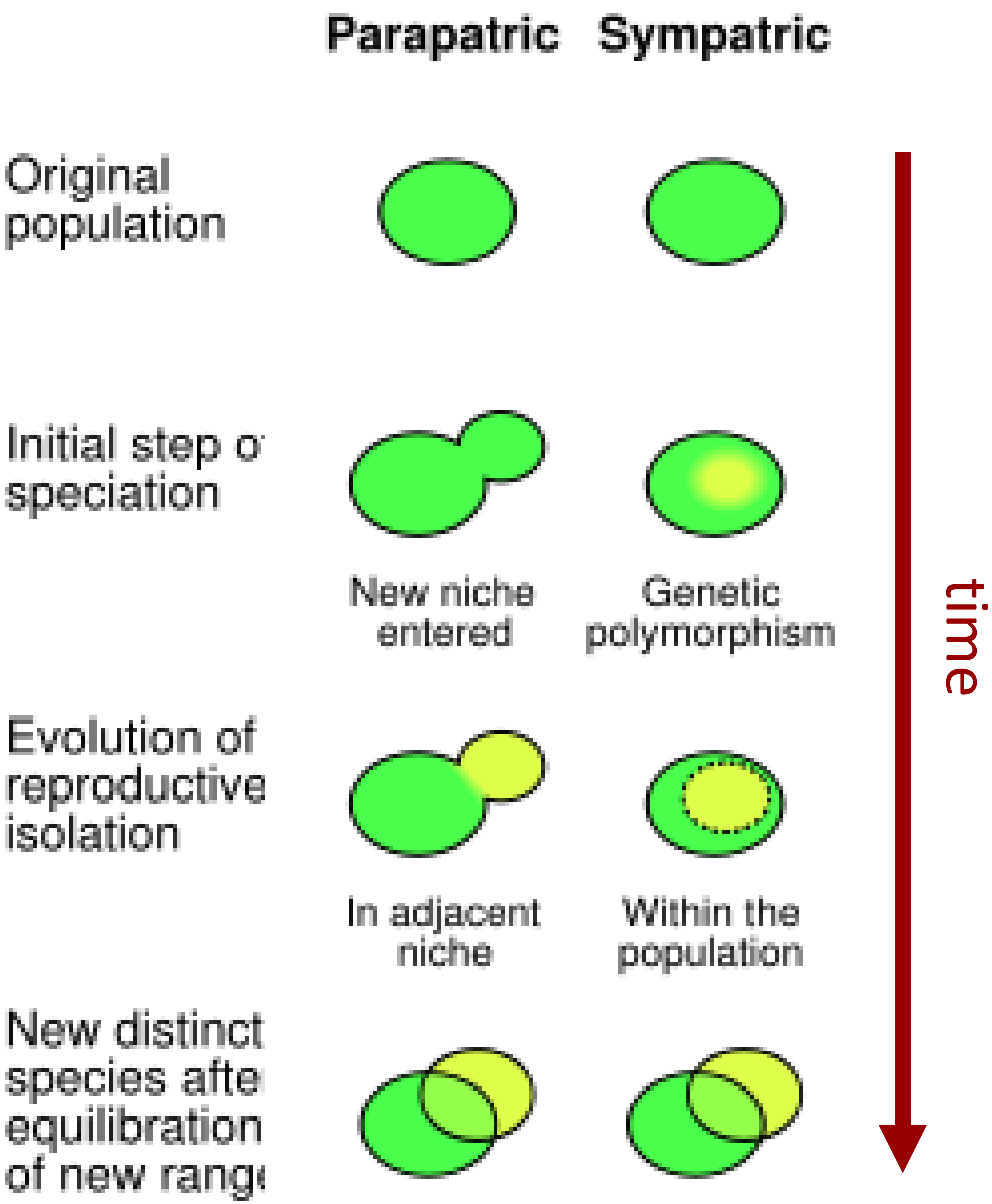
Adaptive Radiation

- Evolution of many diversely-adapted species from a common ancestor:
  - Hawaii.
  - Galapagos.
- Florida Keys too close to mainland.





Models of speciation



The key issue with both of these models is lack of (total) isolation. There is no barrier for gene flow.

It has been shown that the Dobzhansky & Müller model for postzygotic isolation is extremely sensitive for gene flow.

Parapatric speciation?

Parapatric speciation– primary hybrid zone
Allopatric speciation– secondary hybrid zone

hybrid zone

NATURE | VOL 405 | 22 JUNE 2000 | www.nature.com

Formation of secondary hybrid zones in Europe following the Ice Age

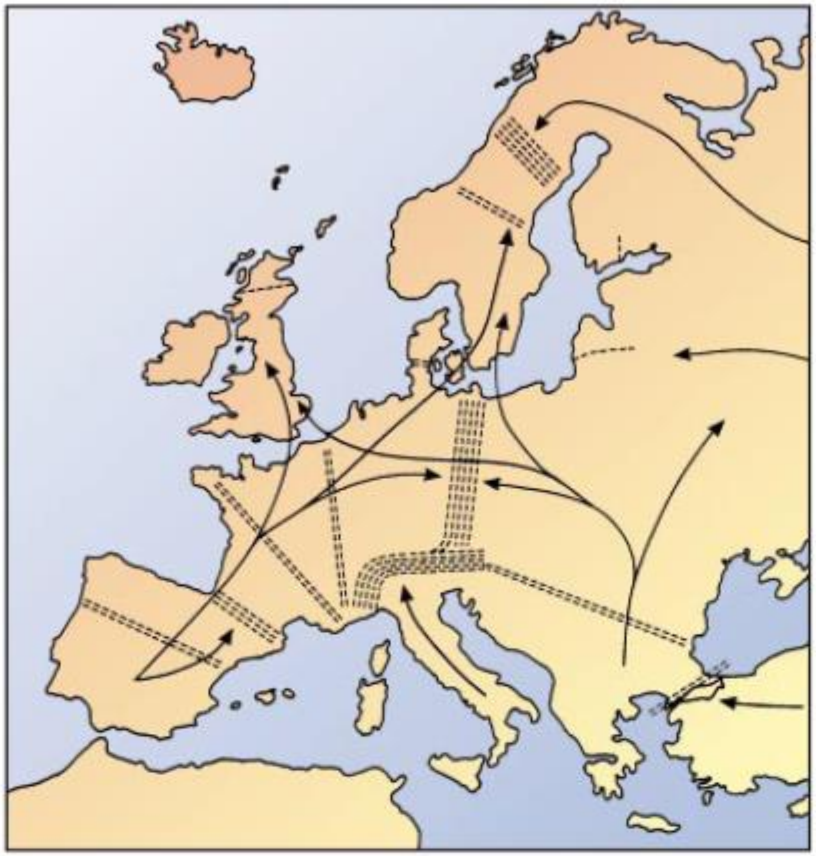


Figure 3 The general position of some well-known hybrid zones in Europe, which show major clustering in Scandinavia, central Europe and the Alps. Other clusters are apparent in the Pyrenees and the Balkans. These suture zones are caused by commonalities of ice-age refugia, rate of postglacial expansion and physical barriers. There is further subdivision in the southern regions.

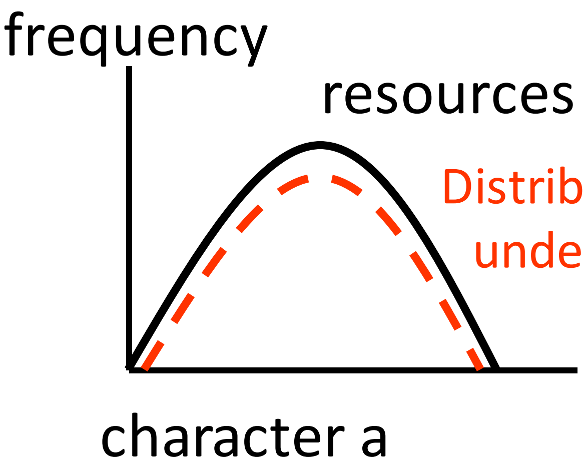
The genetic legacy of the Quaternary ice ages

Godfrey Hewitt

School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK

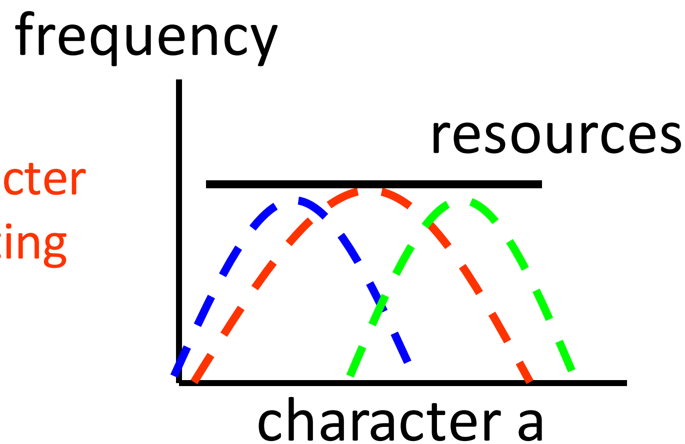
Sympatric speciation?

Theoretically, if the distribution of recources does not match the distribution of genotypes (from random mating) speciation may occur with no geographic isolation



Distribution of character under random mating

~~Synpatric speciation~~



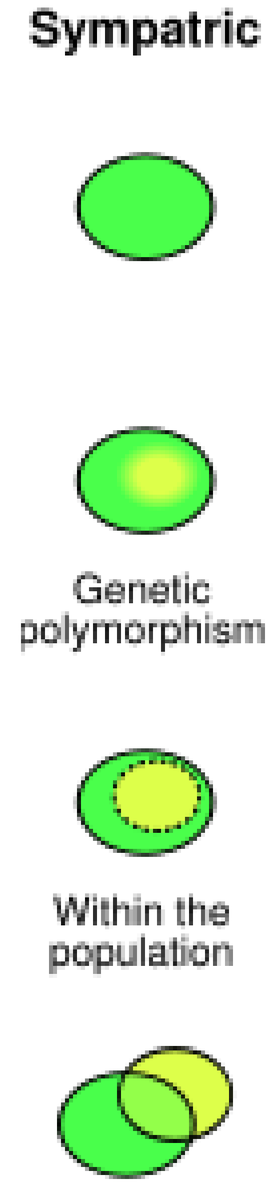
Distribution of character under nonrandom mating

↓

Assortative mating

↓

Synpatric speciation



... Is even more problematic that parapatric.

The main problem is that the disruptive selection and assortative mating must be genetically linked. Recombination will break this linkage eventually even if natural selection would favour it

Speciation

Splitting when together

D Ortiz-Barrientos and LH Rieseberg

Heredity (2006) **97,** 2–3. doi:10.1038/sj.hdy.6800840; published online 17 May 2006

Parapatric and sympatric speciation

1. Non complete or absent geographic divergence
2. Natural selection reinforces speciation

Theoretically sound but hard to show in nature.

In most cases it seems we have:

1. Micro-allopatry
2. Secondary hybrid zones due to cycles of expansion and shrinkage of populated areas