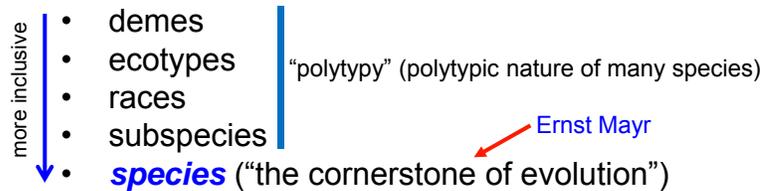


The **Species** is a category of natural variation

Phenotypic variation, based on genotypic variation (V_G), occurs on both spatial and temporal scales.

- Sometimes it's continuous (gradual).
- Sometimes it's discrete.
- Variation can partition diversity into:



What are species, and how do they arise?

First, let's look at *naturally-occurring variation*:

Continuous Variation

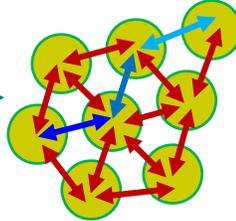
Gradual phenotypic variation over *space* or *time*
e.g., isolation-by-distance or isolation-by-elapsed-time



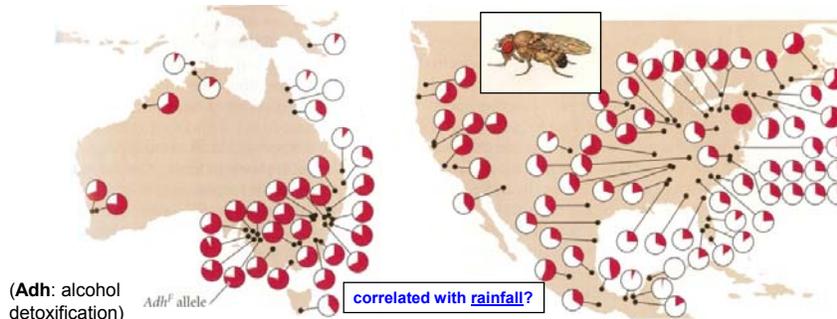
If this arrow is time, then this is *anagenetic change*, expressed as phyletic gradualism.
If the arrow spans space (and this is one species), a case can be made for clinal variation.

Variation is more often than not associated with *geography*.

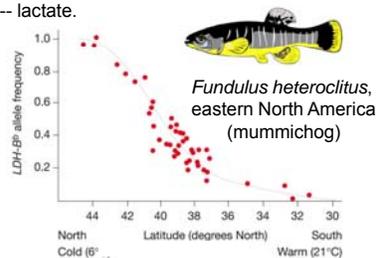
Clinal variation is “*directional*” continuous variation.

- just distance:
 - **isolation-by-distance** → 
 - latitude (distance + environment)
 - altitude (environment)
 - temperature
 - **ecology** (such clines are often narrower) --
 - desert to grassland to forest
 - littoral to benthos
 - one soil type to another (edaphic clines)
 - one host plant to another
- just environment:

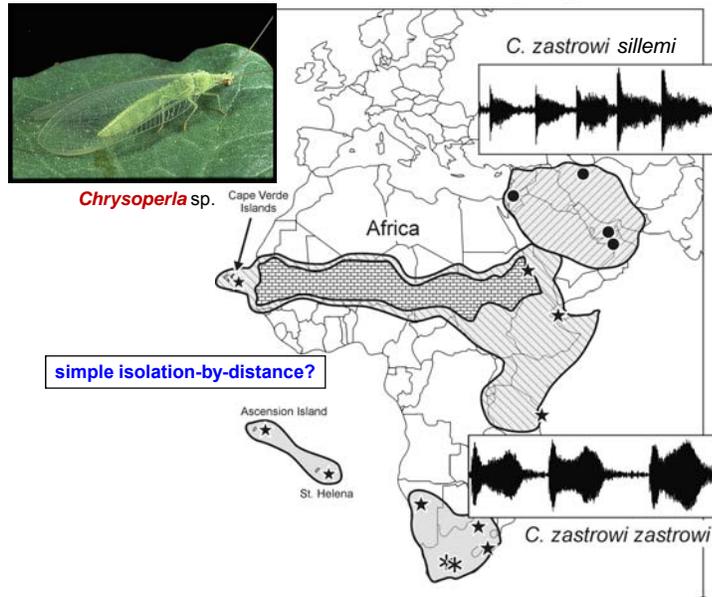
Latitudinal clines: Variation in Adh^F allele in *Drosophila melanogaster* (Oakeshott et al. 1982) and $LDH-B^b$ allele in mummichogs (Powers et al. 1991)



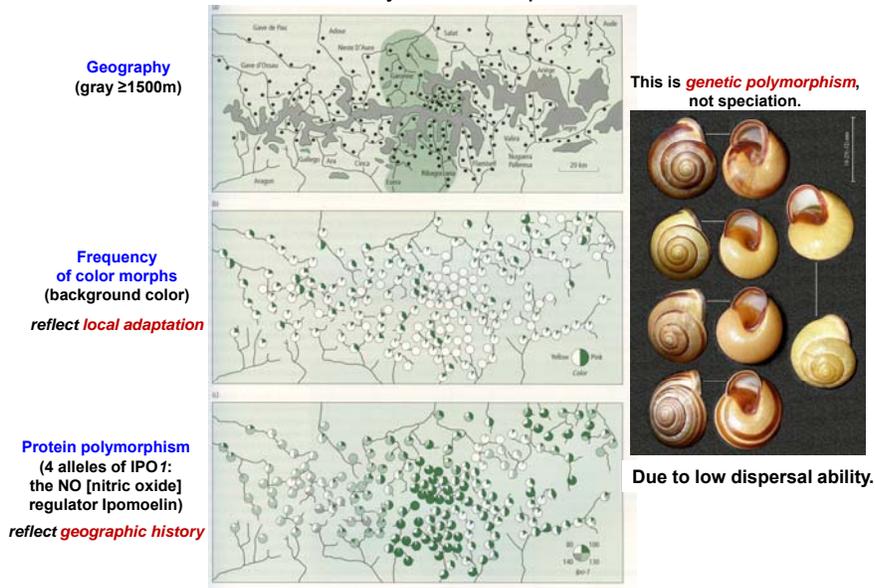
(LDH : respiratory metabolism -- lactate.
correlated with **temperature**)



(Henry et al. 2006, 2010) Clinal variation in the mating song of a lacewing



Non-continuous (discrete or mosaic) Variation:
Land snails of the Pyrenées, *Cepaea nemoralis*



Are species real?



Clustering algorithms that humans use.

- What are they based on?
- Will different humans come up with the same clusters?

Folk Taxonomy (Ernst Mayr's favorite examples)

- Kalám of Papua New Guinea recognize 174 of 178 species of vertebrates recognized by "western taxonomists."
 - Tribes of the Arfak Mountains of New Guinea recognize 136 names for 137 "Linnean" species of birds.
-
- Maybe all humans have a similar "perceptual cluster statistic."
 - Maybe being a species is a way to protect the gene pool from pollution (this assumes "co-adapted" loci and alleles – *group selection?* – see Mallet 2010)
 - You're a "**nominalist**" (or nihilist?) if you think there are *no larger units of classification above the individual.*



Species Concepts (more accurately: hypotheses? definitions?)



- Note that "*species delimitation*" has been conflated with "*species conceptualization*" (de Queiroz 2007).
- Who do we blame for this? – Ernst Mayr, of course; especially his articulation of the "Biological Species Concept" in 1942 (and subsequently).
- Regardless: the debate has forced us to critically consider what we really mean by 'species.'

A classification of species concepts (Rick Harrison 1998)

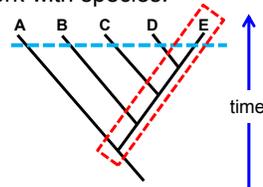
(see also Torretti 2010, Hart 2011, & Singh 2012 for recent reviews)

So is this a *trivial pursuit*?

“It is clear that the arguments will persist for years to come, but equally clear that, like barnacles on a whale, their main effect is to retard slightly the progress of the field.” ---- **Jerry Coyne** 1992

Our “concepts” of species may differ, but we pretty much all understand each other when we describe our work with species.

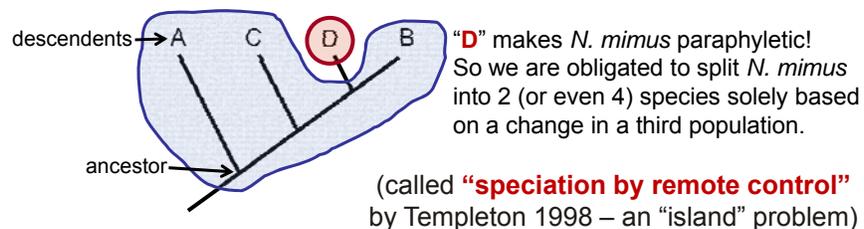
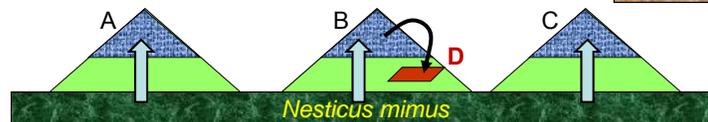
- **Prospective concepts** – based on process.
 - these are necessarily **horizontal** ones.
- **Retrospective concepts** – based on pattern.
 - these can be applied **vertically** as well.



Alan Templeton points out that process generates pattern, so when there's a perceived incompatibility between process and pattern, process should have priority (*process trumps pattern*).

Can process and pattern conflict? *Nesticus* spiders in the Appalachian Mountains (Hedin 1997)


 original distribution A = B = C = *Nesticus mimus*
 after warming D = *N. carolinensis* (troglodytic)



Species Concepts

Instantaneous or Horizontal Concepts (“Prospective”)

- **Typological (Morphological/Phenetic) Species Concepts**
- Biological Species Concept (RIMs)
- Recognition Species Concept (SMRS)
- Ecological Species Concept

Vertical Concepts (“Retrospective”)

- Phylogenetic/Cladistic Species Concept
- Genealogical Species Concept

Integrative Concepts

- Cohesion Species Concept

Incertae sedis

- Evolutionary Species Concept(s)
- Pluralist Species Concepts
- No Species Concept

and others...

- internodal
- Hennigian
- genic
- ephemeral
- unified
- lineage
- hierarchical
- evolutionary
- essentialist



The Typological Species Concept

(Plato? Aristotle? Linnaeus)

An historical artifact, yet relevant

(see **McCabe**, 2011 on essentialism
from a developmental perspective)



- A species is “*an immutable unit, created at the beginning by a God.*”
 - Individuals are imperfect copies of the perfect **TYPE**.
 - Thus, variation within a species are imperfections or “epiphenomena.”
 - It’s most closely related to the **Morphological Species Concept**,
 - **Rationale**: It is a very important concept for working taxonomists.
i.e., we still designate a “**Type**” for each species – the *type specimen* –
although this is often supplemented by a *type series*, *paratypes*,
lectotypes, *neotypes*, etc.
-
- **Drawbacks**: Too arbitrary & subjective? – although Mayr unfairly demonized Plato and deified Darwin, largely to promote the Modern Synthesis (see **Winsor 2006**).

Phenetic (and ecological?) species: Asexual dandelions



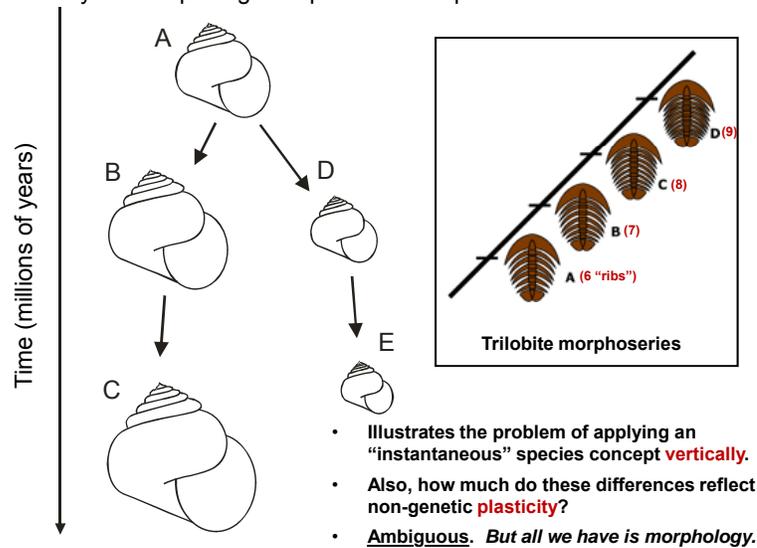
The partially parthenogenetic Dandelions in Europe (*Taraxacum*) have been classified into as many as 70 'microspecies' occupying different habitats.



Note that "folk taxonomy" has *not* worked well with identifying these or other asexually-reproducing species.

Fossils and Chronospecies:

Only the Morphological Species Concept can be used here.



Species Concepts

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- Nihilist Species Concept

The Biological Species Concept

(Mayr 1942, with earlier roots)

- Species are “*groups of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups.*”
- Based on “reproductive isolating mechanisms” (RIMs)

The Recognition Species Concept

(Paterson 1985)

- A species is “*the most inclusive population of individual biparental organisms that share a common fertilization system.*”
 - Based on “shared mate recognition systems” (SMRSs)
-
- **Importance of BSC:** Identifying the species as “a gene pool” placed **systematics** within the conceptual framework of *population genetics* and *microevolution*. Embraces polytypic & cryptic species.
 - **Drawback of BSC:** Assumes “co-adapted gene complexes” and therefore some degree of group-selectionist thinking (Mallet 2010).
 - **Drawbacks to both:** Not applicable to (i) asexually-reproducing populations, (ii) populations that hybridize “too much,” or (iii) populations that don’t overlap in space (allopatric) or time (allochronic).

Hybrid Incompatibilities (intrinsic/genetic postzygotic RIMs)

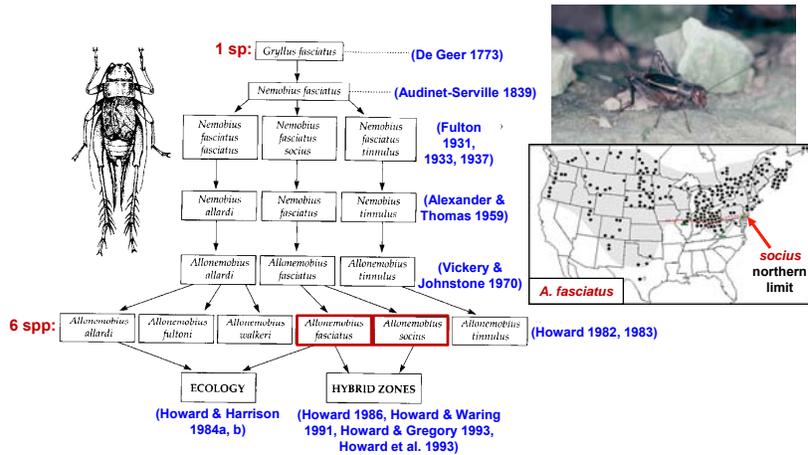
Hybrid breakdown: less viable F₂ hybrids between *Watsonia* species

Reduced F₁ hybrid fertility, or complete hybrid sterility (e.g. donkey x horse = mules & hinnies)

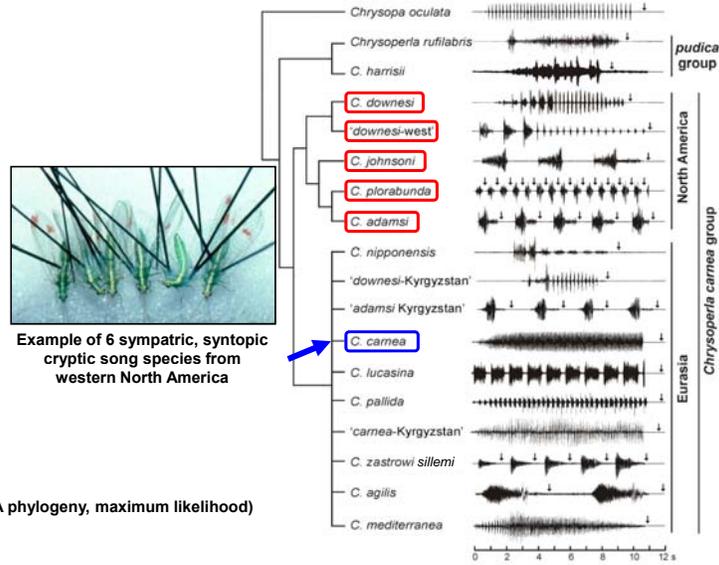


This probably led to loss of interest in cultivating these relatives of the irises as ornamentals (*Watsonia* = bugle lilies; S. African endemics)

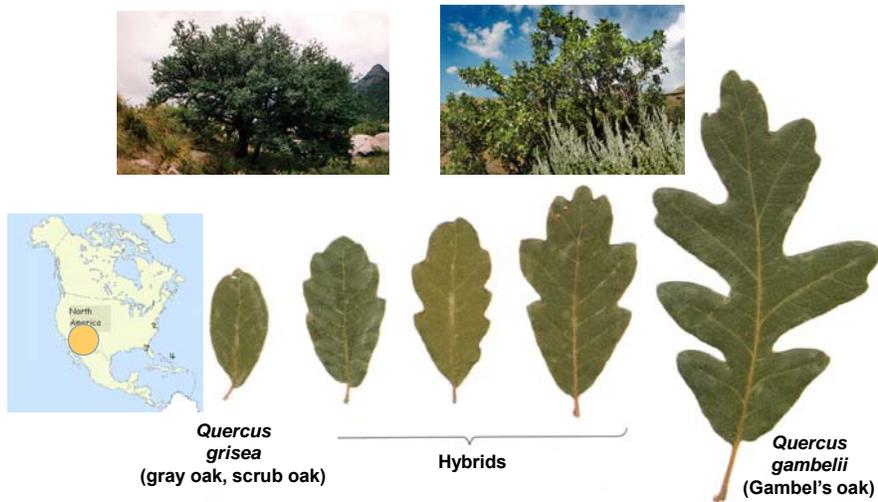
Development of Biological Species Concept for the *Allonemobius fasciatus* complex of crickets over 220 years (based on Howard & Furth 1986, et al.)



The BSC at work: cryptic “song species” of *Chrysoperla*
 From one species (*C. carnea*) to 21 species (Henry et al. 2014)

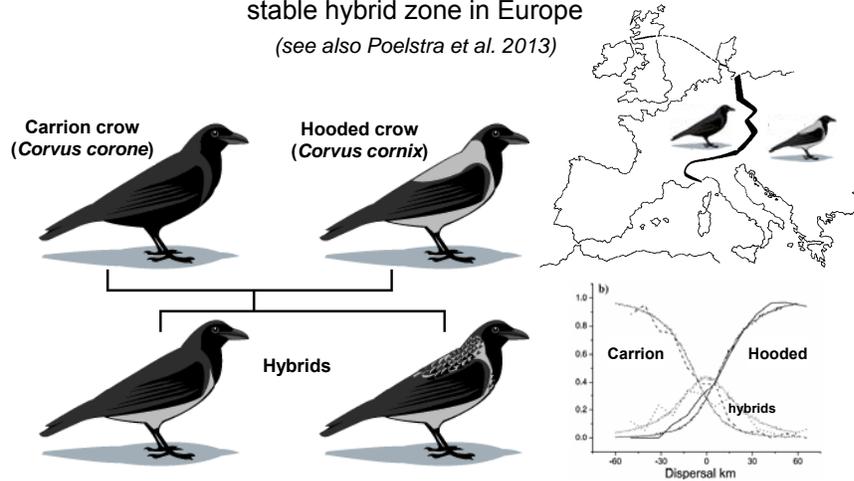


The BSC fails: broad-scale sympatric hybridization.
 A tale of two oaks in the southwestern USA (from Futuyma 2005)



The BSC fails, sort of: Hybridization along a narrow (60km), stable hybrid zone in Europe

(see also *Poelstra et al. 2013*)



- Artificial neural network simulation: stable hybrid zone forms in 60 generations (*Brodin & Haas, 2009*).
- Even with no selection against hybrids; self-recognition alone (sexual imprinting) will generate the same pattern.

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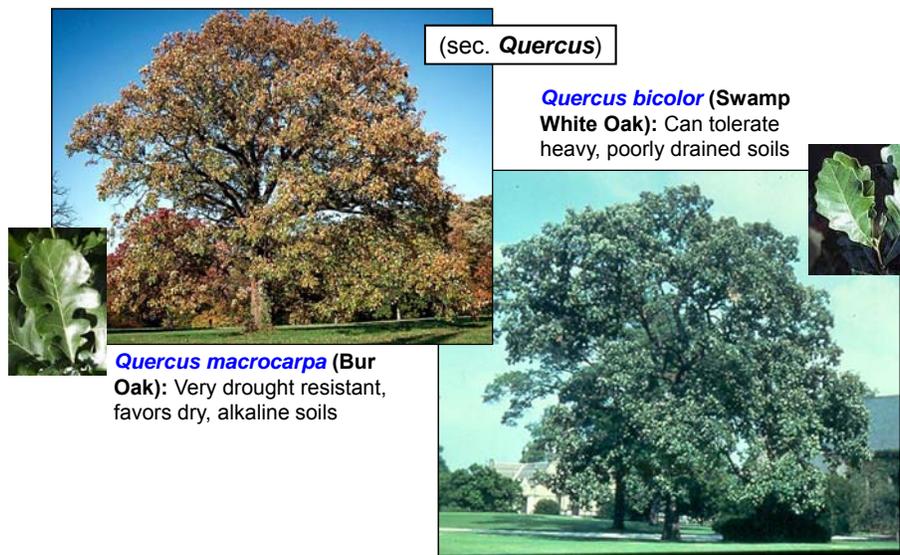
The Ecological Species Concept

(G. G. Simpson; Van Valen; Colinvaux; and others) (Simpson's idea, based on S-Wright)

- A species is “a lineage which occupies an **adaptive zone** minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range” (van Valen 1976) (same as “**evolutionary species concept**” of Simpson)
- **Rationale:** Two closely related organisms sharing the same niche in a given region are likely to be same species.

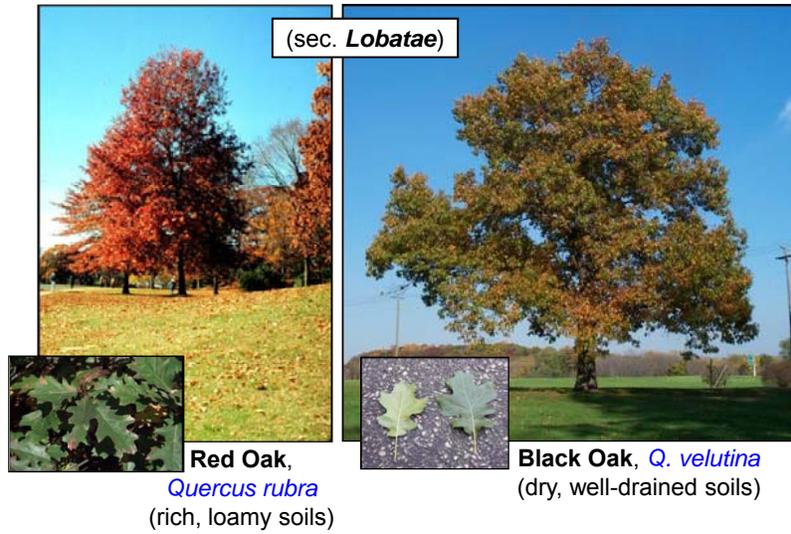
- **Drawbacks:** It requires that members of a single species **not** have variable life histories (niche polymorphism/polytypy **not** good).

Ecological species: Two “white oaks” from eastern N. America

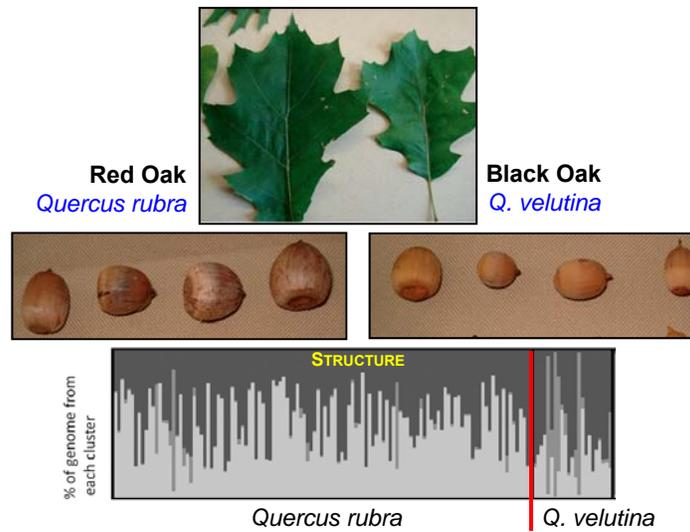


Ecological species, II:

Two “red oaks” from eastern N. America (Moran et al. 2012)



Evidence of **both morphological differences and hybridization** in two “red oaks” from eastern N. America (Moran et al. 2012)



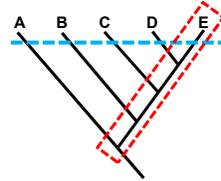
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