"The species problem is like a sword, thrust by Darwin into the stone, and left for us to yank upon with determination and futility." - Hey 2001

Systematics
Lecture 4 - Species

1

Systematics Career Quiz

• Love to look at maps, explore & travel?	4 points
• Picked up bugs, seeds, shells & rocks as child?	3 points
• Well organized?	2 points
• Like to draw?	2 points
• Shy or nerdy as a child?	4 points
• Dream of discovering things no human has seen before?	3 points
• Intrigued by the question, "why are there so many kinds of organisms on earth?"	3 points
• Interested in "relationships"?	3 points
• Good at math & statistics?	2 points
• Blown out hearing listening to loud music?	-1 point**
• enjoy hazardous journeys, small wages, harsh conditions, constant danger, safe return doubtful; Honor and recognition in case of success?	10 points

** Only if you plan to study singing organisms.

If you scored more than 20 points you are a born systematist!
Please explore: www.systematicbiology.org

2

Species - what are they?

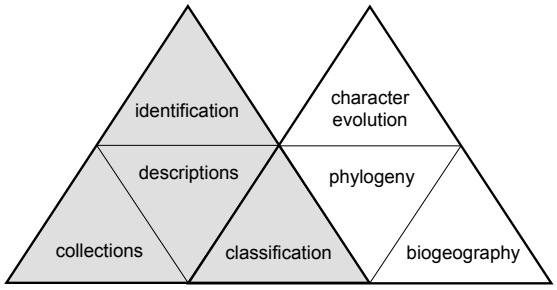
One of the largest & oldest problems in Biology (this lecture is a too-brief summary)

Outline

1. The Species Problem (are they "real"?)
2. Species Concepts - BSC, et al.
3. Speciation - causes

3

Biosystematics



Describing species = assigning names to groups (populations) = classification

4

Biosystematics - readings

Lecture 4: Species & taxonomy

*Sites, J.W., Jr., and Marshall, J.C. (2003). Delimiting species: a renaissance issue in systematic biology. Trends in Ecology and Evolution 18: 462-470.

*Hey, J. (2001) The mind of the species problem. Trends in Ecology and Evolution, 16(7): 326-329.

Mayr, E.& P. D. Ashlock (1991) Principles of Systematic Zoology, 2nd Edition, McGraw-Hill, Inc., NY. pp. 39-54.

*Wilson, E. O. and W. L. Brown (1953) The subspecies concept and its taxonomic application. Syst. Zool. 2: 97-111.

5

Species

- The fundamental unit in biology
- Names are anchors for data retrieval
- Recognition of species is inherent to human cultures
- But biologists still argue about how best to define, or even if species are "real"

6

Historical perspective

Pre 1800s: species were immutable,
"created," *typologists,* e.g. Linnaeus

Variation in nature was considered anomolous

Jean-Baptiste Lamarck (1744-1829) - appreciated variation, considered species to be mutable, evolutionist (but wrong mechanism)

The flood-gates were opening…

7

Historical perspective

After Darwin's 1859 "On the Origin of Species"
variation is key - source of new species

The Modern Synthesis
1930s - genetic basis of variation
birth of population genetics
(gene flow, founder effect, drift…)

1) Dobhanzky's (1937) "The Modern Synthesis"
2) Mayr's (1942) "Systematics and the Origin of Species"

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Species

First: Are species real?

"In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect, but we shall at least be **freed from the vain search for the undiscovered and undiscoverable essence of the term species**."

Darwin (1859)

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Are mountains real?

Of course they are

10

How many mountains?

11

How many mountains?

12

Species

Mountains

"*Land mass that projects well above its surroundings, higher than a hill*"

- Hard to apply consistently in all cases
  e.g. At what exact point are you no longer on a mountain?

- One person's hill is another's mountain

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Species

How many species?

Although difficult to define, like mountains, they are "real" in the same sense

But, like mountains, the *names* of species are concepts of people - circumscriptions - *hypotheses*

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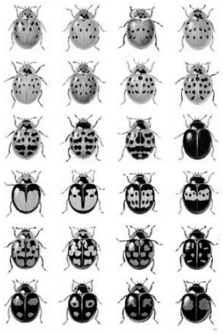
Species

i.e. Species are real but *people decide* where to "draw the line" between species
- we want these decisions to be repeatable

Naturally, disagreement is common

See Hey (2001) "Mind of the species problem"



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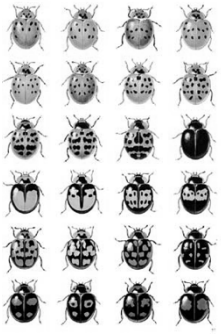
Species

Pattern: observations used

Process: produces pattern - speciation

Different processes can produce species

(like different processes can produce mountains - consider volcanoes versus upthrusts)



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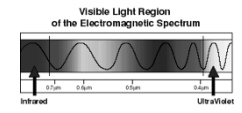
Species

Patterns - recognizing species to give names

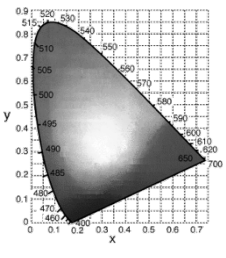
Variation in nature appears to be arranged in *discrete clusters* (at any single place & moment in time)

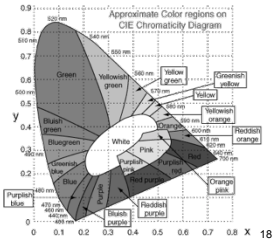
(but some clusters are more discrete than others!)

17



The diagram given here is associated with the 1931 CIE standard. Revisions were made in 1960 and 1976, but the 1931 version remains the most widely used version.





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Species

Patterns - recognizing species to give names

Phenotypic or genotypic gaps
(*nonsexually* linked gaps [Linnaeus])

- can be large / obvious (no problem)

- can be small (= problem)
  - cryptic species: morphologically +/- identical
  - incipient species: "almost species"

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Species

Patterns - recognizing species to give names

- gaps disappear / blur with **time** and **space** (problem)

- single time & space = *nondimensional species* (Mayr)

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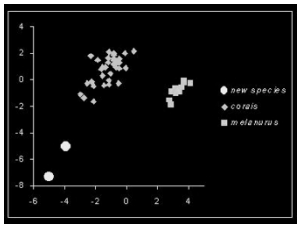
Distinction of species - obvious gap



Multivariate analysis on Indigo snakes - various scale & color pattern characters - new species

From http://biology.bangor.ac.uk/ ~bss166/Taxa/Drymar.htm

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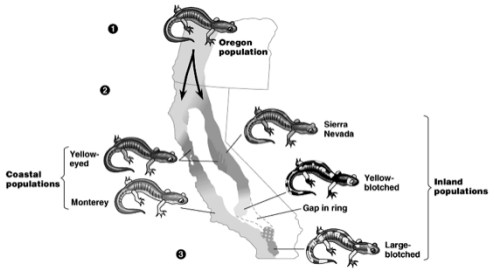
Ring species - incipient speciation [Gap blurs over space]

Continuously breed with adjacent morphs but not across southern range - if intermediates went extinct…



Ensatina eschscholtzii salamander complex

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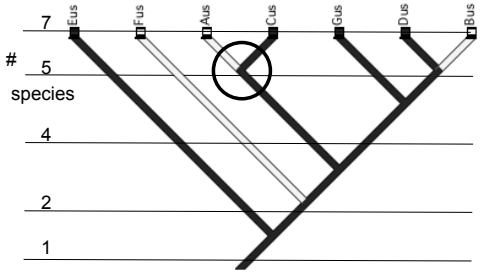
Phylogeny [Gap blurs over time]

"…species distinctions hold only for consideration of a single time transect" - Wilson & Brown 1953



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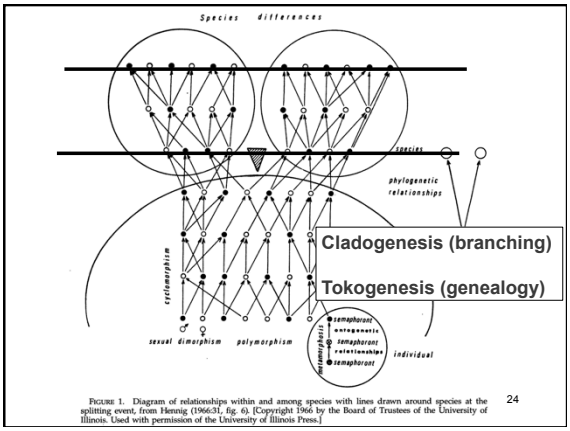

FIGURE 1. Diagram of relationships within and among species with lines drawn around species at the splitting event, from Hennig (1966:31, fig. 6). [Copyright 1966 by the Board of Trustees of the University of Illinois. Used with permission of the University of Illinois Press.]

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Winker, K. 2009. Reuniting Phenotype and Genotype in Biodiversity Research. BioScience 59: 657-665.

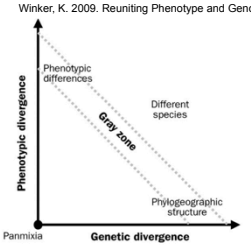


Figure 1. Speciation process space in two dimensions, considering the largely adaptive axis of phenotypic divergence and the largely neutral axis of genetic divergence (adapted from Moritz 2002, and based on traditional biodiversity data sets). Differentiating units progress from panmixia (total genetic admixture) to speciation in this space. The gray zone indicates variation among species concepts about when differentiating units become full species during this process.

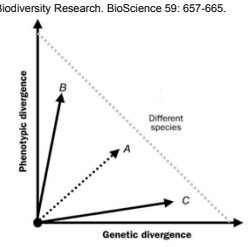
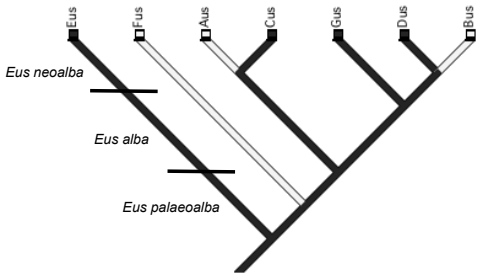


Figure 2. Different routes to speciation possible in the process space of figure 1 (with conceptual variation of "species" arising from different species concepts being collapsed). Route A (dotted line) occurs when phenotypic and genotypic divergence rates are coupled. Differentiation driven largely by adaptive divergence is depicted by route B, whereas that driven by largely neutral divergence is depicted by route C. Route A is dotted because evidence in birds (Zink 2004, Phillimore and Owens 2006) suggests that these two divergence rates are not usually coupled.

Anagenesis (phyletic evolution) - speciation without branching

Seen in the fossil record - chronospecies / paleospecies - time delimited species



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Species Concepts

Assuming species are real…

How do we define them?

- At least 25 different species concepts (Coyne & Orr 2004)
- "Splitters" vs "Lumpers" - concept dependent (read Box 1 Mallet & Willmott 2003) Hey (2001) - 9,000 vs 20,000 bird species?

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Harrison 1998

Concepts for different groups of users:

- *For studying speciation*
  - Process & mechanism
  - Evolutionary groups
- *For organizing diversity* (taxonomy)
  - Pattern
  - To recognize species to give names
  - Names = taxa

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Biological Species Concept

"*groups of actually [or potentially] interbreeding natural populations which are reproductively isolated from other such groups*" – Mayr (1963)

Relies on gene flow isolation

Most well-known species concept

Used in US for Endangered Species Act

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Biological Species Concept

Assumes that if *enough* gene flow is *present* between two populations they are conspecific

i.e. speciation cannot happen in face of gene flow (but what defines "enough")

So simple breeding tests are not adequate (e.g. "We have one case of hybridization in the lab")

One must assess the amount of gene flow in natural populations - difficult work!

(Not possible if populations are widely allopatric eg. monarchs in Australia vs N. America)

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Biological Species Concept

Assumes that if gene flow is *absent* then speciation will occur (if it hasn't already)

"Every geographic isolate is an incipient species" - Mayr & Ashlock '91

Major step forward in biology

These assumptions work to define (what we would like to call) "species" in most, but not all cases

Gene flow is important but is not everything

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Biological Species Concept

	No Gene Flow	Gene Flow
Allopatric	?	1 species or 2 species*
Sympatric	2 species	1 species or 2 species*

* Depending on how much gene flow there is.

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Biological Species Concept - Problems

1. Hybridization

Works well for many, but not all, animals…

- many cases of hybridization
  - e.g. 9.2% of bird species (*Larus* - gulls)
- even over thousands of years

Works poorly for plants

- hybridization far more common
- maintain cohesion despite gene flow

Subjective decision is needed to determine if there is "too much" hybridization

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Biological Species Concept - Problems

2. Fails for paleospecies

Clearly impossible to assess gene flow

Estimates suggest that 99% or more of species are extinct

Emphasizes difference between 'belief' in the BSC and application of it in practice

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Biological Species Concept - Problems

3. Cryptic species - Some good BSC "species" are so young they have not evolved morphological or ecological differences - they apparently differ only in that a mating barrier has developed

e.g. singing organisms, some birds, green lacewings (courtship barrier)

= cryptic species - they look and act identical but belong to different 'breeding' groups

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Biological Species Concept - Problems

4. Asexual species - e.g. Populations of matrilineal clones or bacteria

Each clone-line never exchanges genes with others

They look and act identical but belong to different, isolated, gene-flow clonal lines

But the population maintains its morphological and ecological identity *without* gene flow

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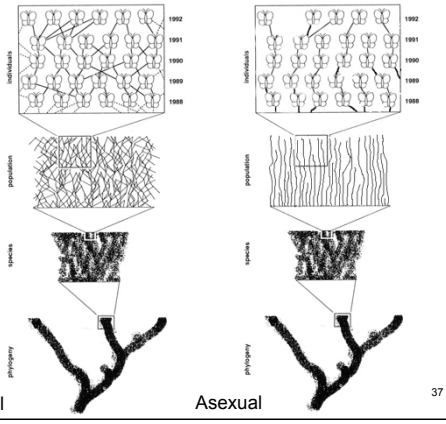

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Biological Species Concept

Many species maintain their cohesiveness despite
- "too much sex" (e.g. *Quercus* [oaks])
- "too little sex" (e.g. rotifers, allopatry)

What maintains the cohesiveness if not gene flow?

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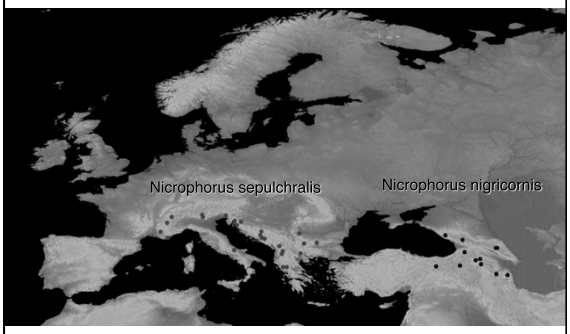
Allopatric species - hard to determine gene flow potential



These sister species differ by color & distribution

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Biological Species Concept

Asymmetrical test (for sexual species):

- intrinsic barriers to gene flow = 2 species
- no (or weak) barriers to gene flow = ?
- ability to interbreed = ancestral
- barrier to interbreeding = derived
  (but does not evolve in all cases)

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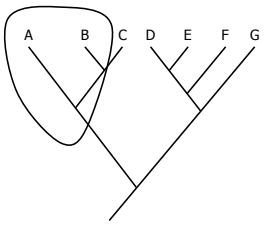
Biological Species Concept

Mating barriers are not 100% correlated with species limits

e.g. Species A & B can breed with each other but neither can breed with C



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Biological Species Concept

Application: (inapplicable to fossils, asexuals, or allopatric species)

- Rarely are actual mating trials conducted or gene flow between populations assessed to determine if barriers to gene flow are present
- Typically, phenotype or genotype is used to infer (hypothesize) presence of barriers
  (which are rarely actually tested)

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Biological Species Concept - In summary

-Grew from a desire to have a simple 'test' to apply to solve the species problem

- Far too many mismatches between BSC and species of nature (& hard to apply)

- It is a poor description of what "species" are

Biological species exist but not all species are biological species

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Other Species Concepts

Harrison (1998): species can be identified by

1) intrinsic barriers to gene flow

2) ecologically distinct

3) diagnosably distinct clusters

4) exclusive (monophyletic) groups

5) independent evolutionary tendencies

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Other Species Concepts

Evolutionary species concept
"A species is a single lineage of ancestor-descendent populations, which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley 1978, from Simpson 1961)

Phylogenetic species concept
"smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals" – Nixon & Wheeler 1990

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Other Species Concepts

New Kid on the Block…

DNA barcodes = [all] species demarcations & future identifications based [only] on sequence data in a 648 base-pair region of the COI gene.

A cutoff of 10x(mean of within-sp. variation) is used to mark the within-species vs among-species split. (birds = 2%)

Simple to use, but does it work?

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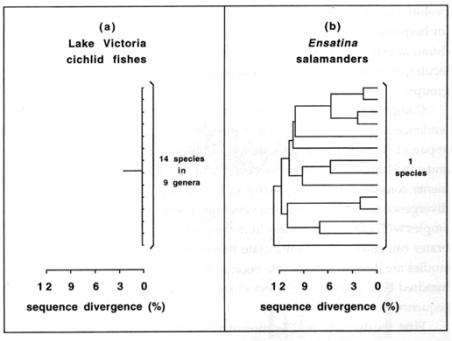
Other Species Concepts



Sites & Marshall (2003): *Ensatina* = 2, 7, or 11 species

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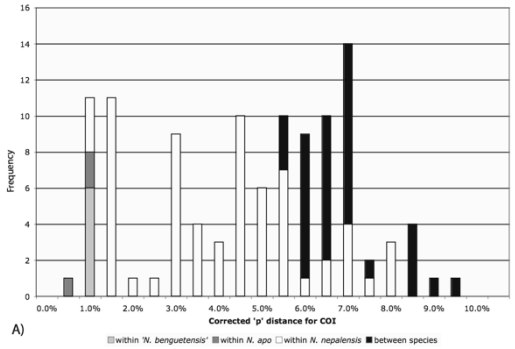
Other Species Concepts



Overlapping within and among species genetic distances

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Speciation - Causes

Enormous volume of work on this subject

Allopatric speciation considered key (BSC)

However, it is slowly becoming clear that speciation (typically) cannot occur without a **change in the selective regime**

Natural Selection working with changes to environment is the key

Allopatry does +/- nothing if environments are identical

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Speciation - Causes

Simple example: Four cages of fruit flies from common gene pool, bred for 5 years

2 cages (A, B) kept in a cold, dark, dry incubator
2 cages (C, D) kept in a warm, bright, humid incubator

After 5 years, mating between all cages allowed
-Random within an environment (eg A-A,A-B,B-B)
-Nonrandom between environments
-Isolation within identical environment had no effect
- thus "allopatry" with same environment is a weaker force for speciation than with different environments.

Kilias, G., Alahiotis, S.N. and Pelecanos, N. (1980). A multifactorial genetic investigation of speciation theory using *Drosophila melanogastor*. Evolution 34: 730-737.

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Speciation - Causes

Adaptation due to Natural Selection working on natural variation yields new species

Sometimes intrinsic barriers to gene flow develop (BSC), but this is not necessary and is certainly not the only *cause* of species formation

Leaves us without a simple test… :(

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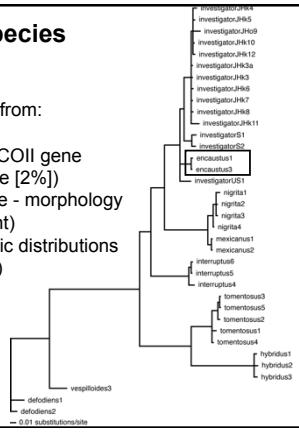
Example species problem

Data (pattern) from:

1. mtDNA - COII gene (+/-same [2%])
2. phenotype - morphology (different)
3. geographic distributions (both…)



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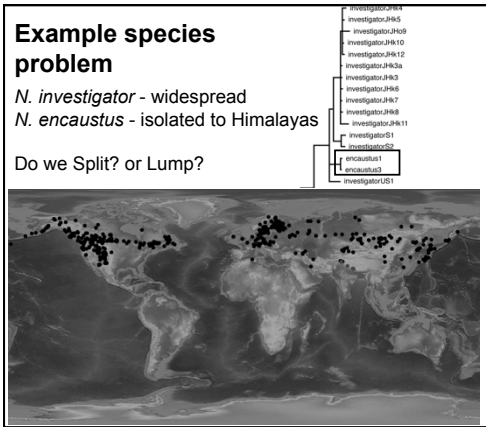
Example species problem

N. investigator - widespread
N. encaustus - isolated to Himalayas

Do we Split? or Lump?



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Wilson & Brown 1953

- Subspecies - use and abuse
- Example of issues of "taxonomic proliferation" = excessive naming / splitting
- Recommend geographic variation be discussed but *not named*

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Wilson & Brown 1953

- Variation is discordant - clusters disagree based on different characters
- **Polytopy** - same phenotype in different / isolated geographic localities, based on environmental conditions
- Microgeographic races - like polytopy but heritable
- Arbitrariness of delimitation - many subspp. based on single characters

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75% subspecies rule (Amadon 1949)

Plumage type	III	IV	V	VI	VI-VII	VII	**VII-VIII**	**VIII**	**IX**	
C. c. canadensis	1	6	5	10	14	25	3	6	0	n=70
C. c. osgoodi	0	0	0	0	2	0	6	6	1	n=15

browner on left, grayer on right
Test 0.75 x 70 = 52.5 observed 64 = pass 75%
Test 0.75 x 15 = 11.2 observed 13 = pass 75%

75% of each subspecies sample doesn't overlap with dianostic trait of other subspecies = "good" subssp.

Since interpreted as "*75% of one group is separable from <u>all</u> in another group*" BUT Not widely used...

Amadon D. 1949. The seventy-five per cent rule for subspecies. The Condor 51: 250–258.

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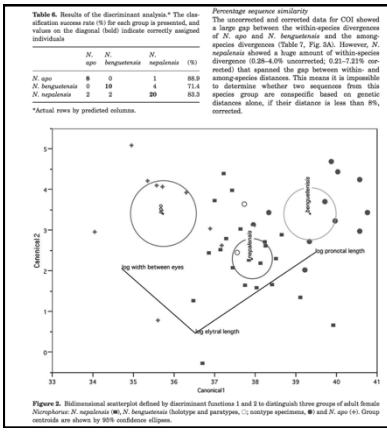

Table 6. Results of the discriminant analysis.* The classification success rate (%) for each group is presented, and values on the diagonal (bold) indicate correctly assigned individuals

	N. apo	*N. benguetensis*	*N. nepalensis*	(%)
N. apo	**8**	0	1	88.9
N. benguetensis	0	**10**	4	71.4
N. nepalensis	2	2	**20**	83.3

*Actual rows by predicted columns.

Percentage sequence similarity
The uncorrected and corrected data for COI showed a large gap between the within-species divergences of *N. apo* and *N. benguetensis* and the among-species divergences (Table 7, Fig. 3A). However, *N. nepalensis* showed a huge amount of within-species divergence (0.28–4.0% uncorrected; 0.21–7.21% corrected) that spanned the gap between within- and among-species distances. This means it is impossible to determine whether two sequences from this species group are conspecific based on genetic distances alone, if their distance is less than 8%, corrected.

Figure 2. Bidimensional scatterplot defined by discriminant functions 1 and 2 to distinguish three groups of adult female *Nicrophorus*: *N. nepalensis* (●), *N. benguetensis* (holotype and paratypes, ○; nontype specimens, ●) and *N. apo* (+). Group centroids are shown by 95% confidence ellipses.

Mousseau, T. and Sikes, D. 2011. Almost but not quite a subspecies: a case of genetic but not morphological diagnosability in Nicrophours (Coleoptera: Silphidae). Biological Journal of the Linnean Society 102: 311-333.

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Summary of key points

Species are both *names* and *things*

1. Names (taxa) are subjective, decisions of taxonomists
2. Names are hypotheses of things
   (linking the subjective with the objective using a Species Concept)
3. Things are objective, (species are products of evolution - "evolutionary groups" [Hey 2001])

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Closing words from Darwin

"*Hence, in determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgement and wide experience seems the only guide to follow*." Origin, Ch. 2

Species do exist but there is no single definition that works for all of them

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Homework Question:

Species - how are they cited / used?

a) As if they are real entities of nature
   or
b) As if they are concepts / hypotheses of their authors

What are some key implications of this?
(e.g. for difficult cases of demarcation?
Or for "image" of alpha taxonomy?)

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Terms - from lecture & readings

Species concept
Splitting / lumping
Speciation
Anagenesis, chronospecies, phyletic evolution
Cladogenesis
Species (ring species, incipient species, cryptic species, sister species)
Subspecies (race, deme, form)
75% subspecies rule
cline

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You should be able to

Describe The Species Problem

Describe if you think species are “real” & why

Describe shift from typological approach to biological

Describe the BSC: its assumptions & problems

Describe role of pattern vs process in species concepts (who uses concepts with which emphasis?)

Why does splitting & lumping of names happen?

Briefly describe speciation

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