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”?)
3. Speciation - causes

Species - readings
Lecture 4: Species & taxonomy


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”

Historical perspective
Pre 1800s: species were immutable, “created,” typologists, e.g. Linnaeus

Variation in nature was considered anomalous

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

The flood-gates were opening…
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) Dobzhansky’s (1937) “The Modern Synthesis”
2) Mayr’s (1942) “Systematics and the Origin of Species”

“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

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

**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!)

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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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**Distinction of species - obvious gap**

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

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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...
Phylogeny [Gap blurs over time]

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

Cladogenesis (branching)
Tokogenesis (genealogy)

Anagenesis (phylectic evolution) - speciation without branching
Seen in the fossil record - chronospecies / paleospecies - time delimited species

Eus neoalba
Eus alba
Eus paleoalba

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?

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

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
Introduction to Biosystematics - Zool 575

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 allopatric)

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

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

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

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
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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**Biological Species Concept**

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

What maintains the cohesiveness if not gene flow?

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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)
Introduction to Biosystematics - Zool 575

**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 (hypothese) presence of barriers (which are rarely actually tested)

**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**

### 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 (e.g., A-A, A-B, B-B)
- Nonrandom between environments
- Isolation within identical environment had no effect

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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
### 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

### 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])

### 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

### 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?)

### 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)
- Cline

### 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