

## Ontology of Evolution: Species, Units, and Levels

---

---

---

---

---

---

---

---

## Natural Kinds

- Kind defined in terms of essential properties
  - All and only entities with the essential properties are instances of the kind
- Essential properties explain the key characteristics of the kind
- From knowing the essence, we can predict the properties associated with the kind



---

---

---

---

---

---

---

---

## Species as Natural Kinds?

- Are any traits necessary or sufficient to species
  - Would a mutant lacking the traits be excluded from the species?
  - Would a mutant of another species that acquired the trait become a member of the species?
  - Are there any sharp boundaries between members and non-members of a species?

---

---

---

---

---

---

---

---



## Species as Individuals



- David Hull and Michael Ghiselin
  - Traditionally species have been construed as types or sets
  - But species are historical entities—they are born and they go extinct
  - In this, they are *individuals*—spatially, temporally extended entities
  - You and I are parts of the species *homo sapiens*, not members of it
- Individual species cannot be the subject of scientific laws

---

---

---

---

---

---

---

---

## Surprising Consequences of Species as Individuals

- If it walks like a duck, quacks like a duck, . . . , but was not born of a duck, it is not a duck
  - And if it is born of a duck, it is a duck even if it doesn't look like a duck, quack like a duck, . . .
- There cannot be ducks, or people, anywhere else in the universe
  - Even if they look just like us, and speak English

---

---

---

---

---

---

---

---

## Individualism and Human Nature

- Many people are deeply concerned to figure out what human nature consists in
  - Language
  - Tool use
  - Sociality
- If species are individuals, there is no human nature

---

---

---

---

---

---

---

---

## Responses to Species as Individuals

- Boyd's Homeostatic Property Clusters: There are a cluster of processes that promote stability (homeostasis) within a species
  - Gene flow
  - Stabilizing pressure
  - Developmental homeostasis
- Pluralism: different species concepts for different purposes

---

---

---

---

---

---

---

---



## Taxonomy Wars



- Phenetics (numerical taxonomy)
  - Attempts to provide an atheoretical taxonomy (neutral between theories)
  - Start with traits and compute similarities
    - Variety of mathematical/statistical techniques recruited to create trees--phenogram
- Cladistics
  - Make phylogeny the key to taxonomy
  - Show order in which different species split from one another
  - Insist on monophyletic groups: A phyla consists of all and only the descendents of a species

---

---

---

---

---

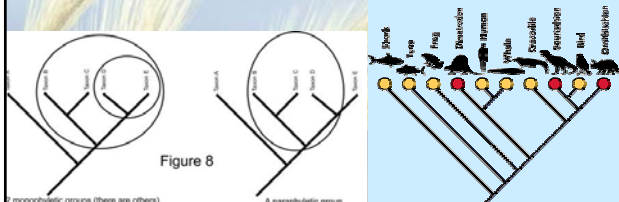
---

---

---

## Cladograms

- Represent species at terminal nodes
- Nodes represent splitting of a common ancestor
- Ancestor species ends at the split
- Higher phyla all monophyletic




---

---

---

---

---

---

---

---

## Some Candidate Accounts of Species

- Phenetic species concept: species are groups defined in terms of overall similarity
- Biological species concept: species are populations that are reproductively isolated
  - Mayr: isolation via "biological properties of individuals which prevent the interbreeding [fusion] of populations"
- Phylogenetic species concept: species are lineages of ancestral/descendant populations between speciation events
  - Hennig: speciation always involves splitting of existing species (which then cease to exist)
- Others:
  - Cohesion species concept
  - Ecological species concept

---

---

---

---

---

---

---

---

## Problems with the Phenetic Species Concept

- What is *similarity*?
  - Any two objects in the universe are similar in an unlimited number of respects
  - Must specify dimensions and metrics for determining similarity
- Members of a species can vary significantly (especially in polytypic species) and members of different species may appear more similar to each other than members of the same species

---

---

---

---

---

---

---

---

## Problems with the Biological Species Concept

- Challenge temporally: depending on which organisms you start with, set the forward and backward limits of the species
- Groups that might not interbreed but easily could and groups that are different despite gene flow
  - Might try *potential* interbreeding, but no way to spell that notion out
- Problems with plants and single-celled organisms
  - Especially asexual organisms: Is each individual a different species?

---

---

---

---

---

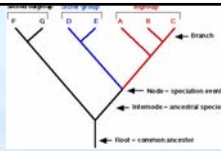
---

---

---



# Problems with the Phylogenetic Species Concept



- Need a means of identifying speciation events and so must use something like break in interbreeding or cohesiveness
- “the most plausible account of species is that they are lineages between speciation events. The biological species concept, perhaps supplemented by the ecological species concept or by something else, reemerges as an account of speciation” (Sterelny and Griffiths, p. 192).

---

---

---

---

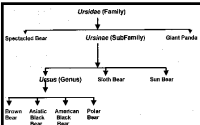
---

---

---

---

# Higher Taxa



- Linnaean Hierarchy
- Three desiderata of a classification system:
  - Position in hierarchy should convey maximal information about the traits of an item
  - Should reflect differences and evolutionary change
  - Reflect phylogeny
- Incompatible desiderata

---

---

---

---

---

---

---

---

# Units and Levels

- What are the units/entities that figure in evolution
  - Population genetics tells the story in terms of alleles in the gene pool
  - Are there any units larger (at a higher level) than genes that need to be considered?
    - Linkage groups?
    - Chromosomes?
    - Genomes?
    - Organisms?
    - Groups?
    - Species?

---

---

---

---

---

---

---

---

## The Gene as Unit of Evolution



- Richard Dawkins:
  - Replicators: That which is directly copied
  - Vehicle: That which houses replicators and serves to protect and propagate them—organisms
    - Vehicles are selected
    - But the gene is the fundamental unit of evolution
- David Hull
  - Replicator: “an entity that passes on its structure directly in replication” (Hull 1980, p.318)
  - Interactor: The which interacts with the environment such that replication is differential
  - Natural selection: “a process in which the differential extinction and proliferation of interactors cause the differential perpetuation of the replicators that produced them” (Hull 1980, p. 318)

---

---

---

---

---

---

---

---

## What Replicates?

- Organisms do not—their traits are broken up in reproduction
- Chromosomes do not—the genes on them can recombine
- Only genes! They are the “indivisible fragments”
- Dawkins: Analyze evolution solely at the genic level
  - Focus on interactors is mistaken
  - An organism is just a gene’s way of making copies of themselves
- But is this the right question?

---

---

---

---

---

---

---

---

## Can Units Higher than Genes be Interactors/Replicators?

- What does selection operate on
  - Genes, chromosomes, gametes, organisms, kin-groups, groups
- Traditional accounts of group selection: group traits can be selected because of the benefit they confer on the group
  - Wynne-Edwards: groups keep the number of offspring low because the whole group will benefit
  - George Williams: groups do not exhibit traits that are the products of natural selection (adaptations)
    - No mechanism for group selection
    - Group selection ineffectual

---

---

---

---

---

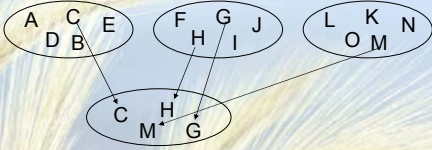
---

---

---

## Strategy for Modeling to Evaluate Group Selection

- Start with several groups of individuals and let them selectively contribute to the pool from which new groups are formed



- Equivalent to blending inheritance
  - The model destroys all the variance on which selection could work

---

---

---

---

---

---

---

---

## Michael Wade and Tribolium

- Offspring groups originate within a single group
- Select between groups for those with low fecundity
  - Within groups greater fecundity wins
  - But overall fecundity goes down
- Why?
  - Within a given group, fecundity more likely to rise
  - But there is variability between groups, and those groups with lower fecundity leave more offspring



---

---

---

---

---

---

---

---

## Simpson's Paradox

- Partitioning a population into two parts can result in a reversal in the direction of relation between two variables
  - The death rate from tuberculosis for African Americans was **lower** in Richmond than in New York.
  - The death rate from tuberculosis for Caucasians was **lower** in Richmond than in New York.
  - The death rate for the total combined population of African Americans and Caucasians from tuberculosis was **higher** in Richmond than in New York.

---

---

---

---

---

---

---

---

## Simpson's Paradox

| Population     | New York  | Richmond |
|----------------|-----------|----------|
| White          | 4,675,174 | 80,895   |
| Black          | 91,709    | 46,733   |
| Combined       | 4,766,883 | 127,628  |
| Deaths         | New York  | Richmond |
| White          | 8,365     | 131      |
| Black          | 513       | 155      |
| Combined       | 8,878     | 286      |
| Mortality rate | New York  | Richmond |
| White          | .179%     | .162%    |
| Black          | .560%     | .332%    |
| Combined       | .186%     | .224%    |

---

---

---

---

---

---

---

---

---

---

## Group Selection for Altruism

| Selfish Group    | Selfish Individuals | Altruistic Individuals |
|------------------|---------------------|------------------------|
| Before           | 40                  | 5                      |
| After            | 20                  | 0                      |
| Altruistic Group | Selfish Individuals | Altruistic Individuals |
| Before           | 5                   | 40                     |
| After            | 8                   | 40                     |
| Combined         | Selfish Individuals | Altruistic Individuals |
| Before           | 45                  | 45                     |
| After            | 28                  | 40                     |

---

---

---

---

---

---

---

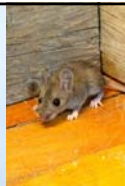
---

---

---

## House Mouse and t-allele

- Evolutionary processes at three levels
  - 80% of the sperm of heterozygotes for the t-allele carry it (normal = 50%)
  - Males homozygotic for the t-allele are sterile
  - Groups with all sterile males go extinct
- Strategy for telling the whole story at the genic level
  - Build in all the higher-level factors into the environment of individual genes
  - "What appears as a multiple level selection process (e.g., selection of the t-allele) to those who draw the conceptual divide [between environments] at the traditional level, appears to genic selectionists of Williams's style as several selection processes being carried out at the same level within different genetic environments" (Waters, 1991, p. 571)




---

---

---

---

---

---

---

---

---

---



## Two Group Selection Questions

- Are there group level traits that are adaptations (products of natural selection)?
  - For Williams, this was important
- Are groups the relevant interactors in the evolutionary scenario?
  - Adaptations may all be at the individual level but groups may be what gets selected
  - Wright, Wade, etc. treat this as the critical question in their defense of group selection

---

---

---

---

---

---

---

---

## Maynard Smith: Resolving Semantic Confusions

"There has been some semantic confusion about the phrase "group selection," for which I may be partly responsible. For me, the debate about levels of selection was initiated by Wynne-Edwards' book. He argued that there are group-level adaptations...which inform individuals of the size of the population so that they can adjust their breeding for the good of the population. He was clear that such adaptations could evolve *only* if populations were units of selection.... Perhaps unfortunately, he referred to the process as "group selection." As a consequence, for me and for many others who engaged in this debate, the phrase came to imply that groups were sufficiently isolated from one another reproductively to act as units of evolution, and not merely that selection acted on groups. . . .



---

---

---

---

---

---

---

---

## Maynard Smith: Resolving Semantic Confusions

"The importance of this debate lay in the fact that group-adaptationist thinking was at that time widespread among biologists. It was therefore important to establish that there is no reason to expect groups to evolve traits ensuring their own survival unless they are sufficiently isolated for like to beget like.... When Wilson (1975) introduced his trait-group model, I was for a long time bewildered by his wish to treat it as a case of group selection and doubly so by the fact that his original model...had interesting results only when the members of the group were genetically related, a process I had been calling kin selection for ten years. I think that these semantic difficulties are now largely over. (Maynard-Smith, 1987, p. 123).

---

---

---

---

---

---

---

---

## Waters and Pluralism



- Many equally adequate representations of the evolutionary process
  - Tell the story at any point in the hierarchy of genes, genomes, organisms, etc.
  - One way to represent the evolutionary process is in terms of genes as agents

---

---

---

---

---

---

---

---

## Bookkeeping vs. Causality



- One might do all the bookkeeping for evolution in terms of gene frequencies in the gene pool
- The causal processes, however, might lie at multiple levels
  - Lloyd: the genic level causal story is derived from accounts characterizing higher-level causes
    - “despite the pluralists' repeated claims, we can see *from their own calculations and examples* that theirs are *derivative* models, and thus, that their “genic” level causes are derivative from and dependent on higher level causes.”
- Strategy for identifying causes—screening off

---

---

---

---

---

---

---

---