

## Ontology of Evolution: Species and Units of Selection

“It is really laughable to see what different ideas are prominent in various naturalists' minds, when they speak of 'species' ; in some, resemblance is everything and descent of little weight — in some, resemblance seems to go for nothing, and Creation the reigning idea — in some, sterility an unfailing test, with others it is not worth a farthing. It all comes, I believe, from trying to define the indefinable” (Darwin, December 24, 1856)

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## Why does it Matter How Species are Characterized?

- Scientifically?
  - Understanding evolution
  - Using species as model systems
- Morally?
  - Is X a human being (in the moral sense)?
  - What obligations do we have to certain organisms?
- Public Policy?
  - Should we protect it?

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## Size of the Problem

Estimated number of species in different orders

- 5–10 million bacteria
- 1.6 million eukaryote species
  - 297,326 plants
  - 28,849 fungi & other non-animals
  - 1,250,000 animals
    - 1,203,375 invertebrates
    - 59,811 vertebrates:
      - 29,300 fish
      - 6,199 amphibians
      - 8,240 reptiles
      - 9,956 birds
      - 5,416 mammals

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## 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

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## 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?

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## 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

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### Surprising Consequences of Species as Individuals

- Individual species cannot be the subject of scientific laws
- 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

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### Individualism and Human Nature

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

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### Responses to Species as Individuals

- Some have found the idea that a species is nothing more than a lineage impossible to accept
  - There must be something more that unifies the individuals in a lineage into a species
- 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
  - For physiology it might be valuable to define species in terms of their traits

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### Some Candidate Accounts of Species

- Phenetic species concept: species are groups defined in terms of overall similarity
- 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)
- Biological species concept: species are populations that are reproductively isolated
  - Mayr: isolation via “biological properties of individuals which prevent the interbreeding [fusion] of populations”

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### 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

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### 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?
  - These are most of the life forms on the planet
    - So, if we stick with the biological species concept, most organisms don't form species

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### 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).

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### The Prokaryote Challenge

- Since Weismann in the late 19<sup>th</sup> century, the dominant view has been that genetic material is transferred only vertically from parents to offspring
- In bacteria, however, lateral gene transfer—transfer of genes from one organism to another is coming to be recognized as quite common
- It appears likely that eukaryotic cells (cells with internal organelles such as a nucleus and mitochondria) resulted from the combining of two prokaryotes (one becoming the mitochondrion or the chloroplast)
- This raise serious problems for the tree of life and phylogenetic construals of species

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### Units and Levels

- What are the units/entities that figure in evolution
  - Population genetics tells the story in terms of competing alleles (genes) 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?

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### 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)

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### 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 even genes are not perfectly replicated
  - And their function is modified by epigenetic processes

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### 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

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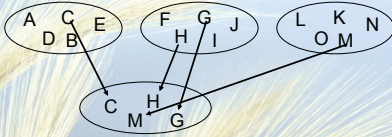
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### Strategy for Modeling to Evaluate Group Selection

- 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
- Yet it was adopted in nearly all models designed to evaluate group selection

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### 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




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### 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.

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### 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%

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### 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

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### 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)

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## 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

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## 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. . . .



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## 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).

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## 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

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## 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

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