Unit 3: Evolution, Genetics, and Development

4. The Ontology of Evolution: Species and Higher-Taxa

"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)

Why does it Matter How Species are Characterized?

- Scientifically?
  - Evolution is, in large part, about what happens to species
  - In many fields, species are used as model systems for understanding other species
- Morally?
  - Is a specific organism a human being (in the moral sense)?
  - What obligations do we have to certain organisms?
- Public Policy?
  - Determining what we should protect

Size of the Problem

Estimated number of species in different orders

- 5–10 million bacterial species
- 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

Natural Kinds

- A kind (or a set) is 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 something's essence, we can predict the properties associated with it
  - consider chemistry as a model—elements are natural kinds
    - from knowing the essence of an element we can determine (to some degree) how it will interact with other elements

Clicker Question

Suppose that a trait were found in all members of a species. Would that alone establish it as the essence of the species?

A. Yes, that would make it the essence of the species

B. No, since observers might not be able to readily identify whether an individual possessed the trait

C. No, since that trait might also be possessed by individuals belonging to other species

Species as Natural Kinds (Sets)?

- Are any traits necessary or sufficient to being a member of a 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?

– Are any of these traits ones from which one can explain their remaining traits?
  - As one can explain the reactivity of an element from knowing its number of electrons

Discussion Question

Do you have an essence?

A. Yes, there is a trait that I, and only I have, and I can tell you what it is
B. Yes, there is a trait that I, and only I, have, but I cannot tell you what it is. I just know there has to be something distinctively me.
C. No. I can change my traits by taking appropriate actions and still be me
D. No. I am a continuing entity from birth to death, but my traits can change over time
E. Other

Species as Individuals

- David Hull and Michael Ghiselin advanced an alternative to the traditional view that species are kinds or sets
  - Where sets are specified in terms of conditions of set membership (i.e., essential properties)
- They argued that evolutionary theory requires treating species as historical individuals—they are born and they go extinct and there is a continuous lineage from the first member to the last
  - Species are spatially, temporally extended continuous lineages
  - Species don't have members but parts
    - You and I are parts of the species homo sapiens, not members of it

Evolution and Individuals

- Ghiselin and Hull are not advancing an analytic thesis or even one that is true for all contexts
- Rather, they are arguing that the conception of species as individuals is needed to make sense of how species are understood in evolutionary theory
  - species can change traits through a process of mutation and selection without becoming new species
  - a new species arises from a previous species through a process of breaking from it
    - once it breaks off, the new species is independent

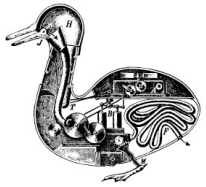
Clicker Question

On the view that species are individuals, which of the following is true of the Dodo Bird (now extinct)

A. A new Dodo bird could evolve in the future
B. Some Dodo birds might have had very different appearances than others
C. There are scientific laws about Dodo birds
D. Dodo birds could have originated independently in different places

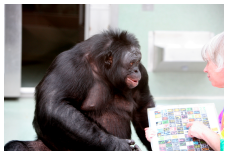
Surprising Consequences of Species as Individuals

- Individual species cannot be the subject of scientific laws
  - Laws refer to kinds of things (e.g., things with a given mass, cells,
  - oxygen), not 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



Species as Individuals and Human Nature

- Many people are deeply invested in trying to figure out what human nature consists in
  - Language?
  - Tool use?
  - Sociality?

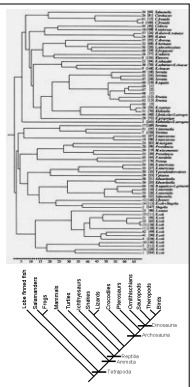


- But, if species are individuals, there is no human nature
  - There is just a lineage of organisms, some of which may differ dramatically from others
    - No matter how many human traits Kanzi acquires, he will never be a human being
      - **for purposes of evolutionary biology**

Responses to Species as Individuals

- Some have found the idea that a species is nothing more than a lineage impossible to accept
  - Devitt argues there must be an essence (intrinsic feature) that determines why the members of a species exhibit the traits they do
- Boyd's Homeostatic Property Clusters
  - Even though there is no one property that all exhibit, there is a cluster of properties that together mark out a species
  - There are processes that promote the maintenance of such clusters within species (gene flow, stabilizing pressure, developmental homeostasis)
  - As a result, species are distinguished by a cluster of properties exhibited by their members throughout their existence
- Pluralism: different species concepts for different purposes
  - Kitcher argues that for proximate explanations (physiology, molecular biology) species are defined in terms of their traits

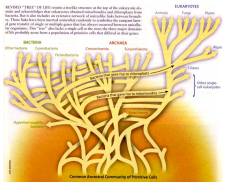
Candidate Species' Concepts



Tools for picking out organisms as parts of a species

- Biological species concept: species are populations that are reproductively isolated
  - Mayr: isolation via "biological properties of individuals which prevent the interbreeding [fusion] of populations"
  - Only works for sexual species (a small minority)
- Phrenetic species concept: species are groups defined in terms of overall similarity
- Phylogenetic (cladist) species concept: species are lineages of ancestral/descendan populations between speciation events
  - Hennig: speciation always involves splitting of existing species (which then ceases to exist)

Prokaryote Challenges



- As a result of lateral gene transfer, the notion of a lineage is not well-defined
  - a given bacterium may have
  - many parents
- Reproductive isolation also doesn't make sense
- What then is a bacterial species?

- In addition to these theoretical challenges, there are practical challenges in identifying bacterial species
  - Typically, to type a bacterium, one grows it in culture
    - but so far we cannot culture most bacterial species
  - One strategy that has been used is to take all the bacteria in an environment, extract and chop up their DNA, and determine which strands can be pieced together into a complete chromosome. Each one is then thought to represent a species

Different but Related Issue: At What Level Does Natural Selection Occur?

- Darwin presented his account in terms of organisms—they were either favored or harmed in reproduction by how adaptive they were to current conditions
- Population genetics made genes the focus—selection favored or counted against genes being passed on
- Are there other levels of organization that figure in Natural Selection?

Communities
Species
Groups
Organisms
Genotypes
Chromosomes
Genes

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Higher Level Organizations in Nature

- Bacterial swarms
  - Individual bacteria no longer "free" to go off on their own
- Eukaryotic cells: formed from the incorporation of one bacteria into another (or into an Archaea)
  - Bacteria provided mitochondria and chloroplasts
  - These organelles lost their independence when they became components of larger cells
- Multi-cellular organisms
  - Division of labor as different cells specialize in different functions (blood cells in carrying oxygen, neurons in transmitting action potentials)
  - But none is able to live independently
    - Cancer: individual cells breaking free of the yoke of being part of a overall organism that restricts its reproductive potential
- Organized groups of organisms in which tasks are distributed

Discussion Question

Being a member of a group (e.g., a political party, a monogamous relationship) often restricts an individual's freedom. Why would individuals do this?

A. They also gain from the fact that the group can accomplish more than solo individuals
B. They believe in the goals promoted by the group
C. They feel coerced into being a member of the group
D. They don't realize that they are missing out on benefits they would have had if they had stayed independent
E. Other

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At What Level Does Natural Selection Occur?

- In *The Descent of Man* Darwin focused on altruism and on how the sacrifice of individuals helped their group at their own expense
- Wynn-Edwards proposed that animals restricted their own reproduction to benefit their group
- Williams (1966) replied, arguing against group selection
  - Organisms don't gain from promoting others in their group
    - They will leave fewer offspring and their traits will soon disappear
- He maintained that all selection occurs at the level of genes
- This set up the question: Are there any units larger (at a higher level) than genes that need to be considered?

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The Gene as the Unit of Evolution

- In *The Selfish Gene* Richard Dawkins:
  - Replicators: That which is directly copied
  - Vehicle: That which houses replicators and serves to protect and propagate them—organisms
    - Vehicles are what interact with the environment
    - 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 entity 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)

Two Questions: What is Selected? Who Benefits

- Dawkin's argument focuses on the beneficiary. We will return to this
- What would it be for selection to promote based on units higher than the gene?
  - If higher-level traits map onto lower-level ones, then there is no gain to focusing on higher levels. Just calculate the benefit each gene brings (population genetics)
  - But if the higher-level trait only arises through the interaction of lower level units, they could be what is promoted by selection
    - Running requires the interaction of many traits of the organism. Genes don't run. Runners win races
    - Producing a play requires the interaction of actors, stage hands, directors, etc. A single actor does not make a play (usually). Plays draw audiences, influence viewers, etc.

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House Mouse and t-allele

- Illustrated by t-allele in the house mouse. The t-allele is
  - Favored at the level of sperm: 80% of the sperm from heterozygotes carry the t-allele (normal = 50%)
  - Selected against at the organism level: Males homozygotic for the t-allele are sterile
  - Selected against at the group level as groups with all sterile males go extinct
- At different levels selection seems to be working in opposite directions but all the effects accrue to the same unit, the t-allele

What Replicates?

- Organisms do not—their traits are broken up in reproduction
- Chromosomes do not—the genes on them can recombine
- So apparently only genes! They are the "indivisible fragments"
  - Dawkins: Analyze evolution solely at the genic level
    - It is a mistake to focus on organisms (interactors) since they are not what benefit from selection
    - An organism is just a gene's way of making copies of themselves
      - It interacts and undergoes selection, but
      - All benefit accrues to the genes (e.g., the t-allele)
    - Crespi takes this view
- But even genes are not perfectly replicated
  - And their function is modified by epigenetic processes
- Should we rethink the conclusions above?

Clicker Question

Using the criteria set out by Williams and Dawkins, what would it take to show that selection operates on a higher level than genes

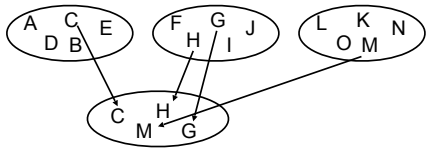
A. That genes are not the units that interact with selection forces in the environment
B. That genes are not replicators
C. That genes are located on chromosomes
D. That entities at a higher level of organization than genes (organisms, groups) replicate and benefit from Natural Selection

Group Replication

- The tendency is to think of groups replicating as nothing more than their individuals replicating
  - The replication of a political party appears to be just a matter of its membership—it succeeds if it adds more members
- Think again. Individual replication does not involve growth of mass
  - For one of us to replicate is for us to produce offspring individuals
- How does that apply to groups?
  - A group replicates if it gives rise to new groups
  - That requires the existing group to divide

Modeling Group Selection

- So what? What matters is which individuals/genes are more prevalent in the future
  - Using mathematical modeling, theorists demonstrate that group selection was impotent
  - Conclusion: selection at the individual/gene level is what drives evolution
- Population genetic models all approached the problem by starting with several groups of individuals and selectively chose from them those that would contribute to the pool from which new groups are formed
  - Groups were not dividing into new groups
  - This mirrors Darwin's fatal account of heredity
    - Variation is lost and so natural selection is powerless



Michael Wade and Tribolium

- Wade performed an experiment with flour beetles
  - Offspring groups originate within a single group —ABSOLUTELY REQUIRED
  - Within groups, the most fecund leave the most offspring
  - Groups with low fecundity—Wade simply eliminated those with the most fecundity
  - He found that overall fecundity declined
    - What was selected for at the group level won
- Why?
  - Although within a given group, fecundity was more likely to rise, that was swamped by the promotion of groups with least fecundity

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.
- While not a strict analog of group selection, Simpson's paradox provides an intuitive understanding of how something can be favored in sub-populations, but selected against in the whole population (or vice versa)

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

Individuals and Groups

- If groups are just collections of individuals, then there is no reason to take groups into account in explaining what happens
- For it to be necessary to consider groups, being part of a group must make a difference to the fitness of an individual
  - If one's fitness is dependent on the group to which one belongs, then it is groups that matter for determining what will happen
- As Brandon notes, this now becomes an empirical question
  - How much of what happens in evolution is due to
    - intrinsic features of the lower-level entity
    - features that entity has only as a result of being part of a higher level unit