Bio 120: Adaptation & Biodiversity
Exam Study Notes (Lectures 12-23)

LECTURE 12: INTRODUCTION TO EVOLUTIONARY BIOLOGY

1. Evolution
2. How it is studied
3. Facts supporting Evolution
4. Biodiversity & adaptation

Levels of biological organization:
Molecules → Cells → Organisms → Populations → Communities → Ecosystems
Types of questions in evolutionary biology:
- **Scope**: small questions can help towards solving a big question; large questions require multiple lines of evidence
- **How vs. Why**
  - **How** → Proximate → Involve determining physiological or genetic **mechanisms**
  - **Why** → Ultimate → Determine ecological **function** and significance of a trait

Approaches used in evolutionary biology:
Good studies use more than one source of evidence
- **Observation** – describe and quantify
- **Theoretical** – develop models
- **Comparative** – compare data across species
- **Experimental** – manipulate a system to address a hypothesis → Requires design and statistical analysis

Theory of Evolution
- The central unifying concept of biology
- Affects many other areas of knowledge
- One of the most influential concepts of Western thought

Important assumptions about evolution: → Verified by scientific study (see Coyne notes below)
- Organisms on earth have changed through time
- The changes are gradual not instantaneous
- Lineages split or branch by speciation resulting in the generation of biodiversity
- All species have common ancestors
- Most evolutionary change results from natural selection - the only process responsible for the evolution of biodiversity and adaptation

Biodiversity and adaptation are products of evolution:
Biodiversity
- the variety of life on earth; the number and kinds of living organisms in a given area

Adaptation
- [Noun] Any trait that contributes to fitness by making an organism better able to survive or reproduce in a given environment
- [Verb] The evolutionary process that leads to the origin and maintenance of such traits

The best studies integrate information from evolutionary history AND mechanisms
Evolutionary mechanisms (microevolution)
- Determining the ecological and genetic mechanisms responsible for evolutionary change

- Involve population-level studies of natural selection, adaptation and speciation using diverse organisms
- Testing of theoretical models by experiments in the laboratory and field
- Largely **process orientated** and **experimental**

Evolutionary history (macroevolution)
- Determining evolutionary relationships of organisms in terms of common ancestry - phylogenetics
- Affinities of organisms provide a basis for classification – taxonomy & systematics
- Comparative data from many sources e.g. biogeography, paleontology, morphology, development and genomics
- Largely **pattern-based** and **non-experimental**

Water Hyacinth
- Novel adaptation promotes outcrossing
- Patterns of genetic diversity
- Blocks drainage canals and rivers
- Short-styled **morph** restricted to lowland S. America through **Founder effect**, by human introduction
- **Morph:** mating type
- **Founder effect:** introduction of a small number of individuals with a small sample of genetic diversity of source population
- Distributed world-wide in tropics and sub-tropics
- Reproduces by clonal and sexual reproduction
- Three morphs restricted to native range

Birds as pollinators
- Birds are major plant pollinators
- Hovering (NW) vs. Perching (OW) birds during nectar feeding
- Some plants, such as Babiana ringens (Rat's tail) have adapted specialized perches for birds promoting plant reproductive success

Reading Summary: Notes and quotes from Coyne - Chapter 1

- "Plants and animals seem intricately and almost perfectly designed for living their lives"
- "It testifies to (Darwin's) genius that the concept of natural theology, accepted by most educated westerners before 1859, was vanquished within only a few years by a single five-hundred page book"
- "Life on earth evolved gradually beginning with one primitive species –perhaps a self-replicating molecule—that lived more than 3.5 billion years ago; it then branched out over time, throwing off many new and diverse species; and the mechanism for most (but not all) of evolutionary change is natural selection"

Evolution
- A species undergoes change over time

Gradualism
- It takes many generations to produce a substantial evolutionary change, such as the evolution of birds from reptiles

Speciation
- Diversity arises through speciation

Common ancestry
- Every species goes back to a single common ancestor

Natural selection

- Explains apparent design by nature
- "If individuals within a species differ genetically from one another, and some of those differences affect an individual's ability to survive and reproduce in its environment, then in the next generation the "good" genes that lead to higher survival and reproduction will have relatively more copies than the "not so good" genes"
- Over time the population becomes more suited to its environment through helpful mutations
- Note that it is not a perfect process – See Sea turtle and human male analogy -- Natural selection merely offers improvements over what came before, therefore it produces "fitter" not the "fittest"

Processes other than natural selection can cause evolutionary change

- Random events – some families have more offspring

Scientific Theory

- A well though-out group of propositions meant to explain facts about the real world
- Explain "**how**" and "**why**" questions
- Must be testable and make verifiable predictions

"Retrodiction"

- When facts and data only make sense in light of a particular scientific theory

LECTURE 13: DARWIN'S BIG IDEA AND HOW IT CHANGED BIOLOGY

1. Evolution - the central unifying concept of biology
2. Development of Darwin's idea
3. Evolution facts and fiction

The theory of evolution

- Living things change gradually from one form into another over time
- Challenges view of special creation (= direct creation of all things in effectively their present form)

Theory of evolution involved two controversial ideas

- Concept of a changing universe → replaced view of a static world
- A phenomenon with no purpose → replaced view that the causes of all phenomena had to have a purpose

Jean-Baptiste de Lamarck (1744 -1829)

- First to use the term evolution
- First to provide a causal mechanism → The inheritance of acquired characters
- **Linear** view of evolution (think LADDER of life, rather than TREE)
  - → Simplest forms evolve directly to complex forms
- The giraffe's neck: Lamarck's example for the inheritance of acquired characters
- Progressive increase in neck during the life time of an individual is passed on to offspring
- Would imply that a weightlifter would give birth to a well-defined and muscled baby, which is simply not true

August Weisman (1834-1914) Germplasm Theory

- Inheritance only by germ cells (gametes); somatic cells (soma) do not function as agents of heredity
- Thus genetic information cannot pass from soma to gametes and onto next generation
- Modern interpretation stated in molecular terms genetic information flows in one direction only from DNA to protein but never in reverse

Discovery of the correct mechanism:

- Charles Darwin & Alfred Russell Wallace co-discover the chief mechanism of evolution: Natural selection

Charles Darwin (1809-1882)

- Darwin influenced by the botanist John S. Henslow at Cambridge
- Darwin reads Charles Lyell's (1797-1875) book "Principles of Geology" (1830)
- **Lyell argued** that present day geological processes can explain the history of the earth – **gradualism**
- The notion of a dynamic rather than a static world emerged in Darwin's thinking
- Voyage on H.M.S. Beagle around the world (1831-1836) as ship's naturalist
  - → Most time spent in South America
- Made numerous observations and collections of plants, animals & fossils
  - → Geographical distribution of plants and animals of oceanic islands
- Returned to England and spent the rest of his life (1842-1882) in seclusion at Down House developing his ideas, conducting experiments and writing books (25 in all)
- Develops the notion that **species vary** based on variation patterns of **Galápagos mockingbirds**
  - → Darwin doubts "fixity" of species (March, 1837)
  - → There are 4 similar species endemic to the islands descended from a South American mainland ancestor

- Darwin reads **Malthus'** (1798) Essay on the Principle of Population (Sept 1838) which influences his notion of **selection**

- 1844: wrote but did not publish an essay on natural selection
- 1856: began work on natural selection book
- June 1858: received "On the tendency of varieties to depart indefinitely from the original type" by A.R. Wallace
- July 1858: Linnean Society presentation in London of Darwin–Wallace paper
- 1859: publication of "The origin of species by means of natural selection or the preservation of favoured races in the struggle for life"

The Origin of Species

- All organisms have descended with modification from common ancestors
- The major agent of modification is natural selection operating on variation among individuals

The essence of a Darwinian world-view

- Recognition that variation among individuals is not imperfection, but the material from which natural selection fashions better adapted forms of life
- This involves a move away from typology and the notion of an ideal species to population thinking

Requirements for Darwin's theory to work – Assumptions

- **Variation** – variation among individuals in a population
- **Heredity** – progeny resemble their parents more than unrelated individuals
- **Selection** – some forms better at surviving and breeding than others in a given environment

Creationist Doctrine

- Literal reading of Book Genesis
- Creation of all living organisms by divine order in 6 days
- All types of organisms individually created and designed by a purposeful creator
  - → Incompatible with evolution
- It is not supported by any empirical observations
- It does not infer its principles from observation, as does all science
- Its assumptions lead to no testable or falsifiable hypotheses

LECTURE 14: WHAT DARWIN SAW: A BIOGEOGRAPHICAL PERSPECTIVE ON BIODIVERSITY AND ADAPTATION

1. Contrasts between tropical & temperate ecosystems
2. The role of biotic and abiotic interactions in temperate and temperate ecosystems, respectively
3. Galápagos Islands as evolutionary laboratories
4. Australia's isolation and its unique biota

During the voyage of the H.M.S. Beagle (1831-1836) → Spends most time in South America

- Stops in **Brazil**
  - → Darwin notes high species diversity and novel adaptations

Tropical Forests in Brazil

- Very high species diversity of plant and animal groups compared with temperate zone
- Many more **biotic** interactions, especially coevolved **mutualisms** between plants and animals
- Year-round warmth results in rapid growth of insect and microbial populations
- Pest and disease pressures on plants more intense

Tropical trees are largely animal-pollinated

Tropical Forests	Temperate Forests
High species diversity	Low species diversity
Individuals of same species widely separated	Individuals of same species close together
Largely Evergreen	Largely Deciduous
Dense canopies	Sparse canopies
Bee, butterfly, moth, bird and bat pollenators	Wind

Daniel Janzen: Euglossine Bees as long-distance pollinators of tropical plants (Science, 1971)

- Used mark-recapture techniques to demonstrate that bees travel up to 23 km during a day
- Today widely recognized that bees, moths and hummingbirds travel long distances during "trapline" foraging
- Janzen's **pest pressure hypothesis**:
  - → Predicts that tropical tree seedlings are less likely to establish close to the maternal parent
    - → Result confirmed through field experiments
  - → Adult tree will have more pests on it, which will transfer to seedlings
  - → Although seedlings are most dense close to parent tree, seedling survival is highest at a greater distance

Acacia

- Intense herbivory in tropical ecosystems results in considerable damage and consumption of plant biomass
- Some species of Acacia and ants have co-evolved to deal with this situation
- Symbiosis: Ant-plant mutualism in Acacia
  - → *Pseudomyrmex* Ants protect Acacia against herbivorous insects
    - → Manipulated with chemicals to keep ants off experimentally
  - → Hollow thorns provide a nesting site for ants
  - → Beltian bodies of Acacia provide protein and lipids while extrafloral nectarines provide sugar for the ants
- Experiment by Megan Frederickson (EEB) (Nature, 2005)

- → Demonstrated that in "Devil's garden," Peru -- ants defend their hosts against plant competitors using formic acid as a herbicide, thus benefitting from more nest sites

Epiphytes:
- Epiphytes are plants that grow on other plants non-parasitically
- Common in the tropics, increasing species diversity
- Epiphytic life form has evolved independently in many unrelated families → Convergent evolution
  - → Ex: Lichens, orchids, bromeliads, mosses
- Questions:
  - → Are particular Trees favoured?
  - → How are they dispersed?
  - → What pollinates them?
  - → How and why have they evolved?
- Bright colours tend to attract pollinators

Opportunities to investigate function and adaptive significance
- Why do some flowers change colour?
- Why are some leaves red?
  - → May protect against herbivory by insects as they don't see red well
- Why does mimicry occur?
  - → Preying mantis – mimics living leaf
  - → Katydid – mimics dead leaf
- Why does poinsettia have red bracts?
  - → May serve to attract pollinators

Finds fossils of extinct mammals – *Glyptodon* – giant armadillo
- Processes that occurred in the past → Extinction

During the voyage of the H.M.S. Beagle (1831-1836)
- Heads south to **Patagonia**

Patagonia
- Discovers strikingly different environments
- Abiotic factors dominate → Completely contrasted by biotic factors of Brazil
  - → Wind shear and ice storm activity affect treelines
- Landscapes are geologically young
- Abiotic factors
- Finds familiar and unfamiliar animal groups, animals with relatives around the world
  - → Black-necked swan → Looks familiar, why is the neck black?
  - → Southern rufous bumblebee → Looks familiar, why is it so fuzzy? Thermoregulation?
  - → Darwin's rhea → Flightlessness evolved
  - → Guanaco → Related to camel?

During the voyage of the H.M.S. Beagle (1831-1836)
- Heads west to **Galápagos Islands**
  - → First arrives on San Cristobal Island (Chatham) on 9/17/1835

Galápagos Islands
- 15 main islands of volcanic origin; oldest 5-10 million years old; youngest more recent
- Flora and fauna colonized by species capable of long-distance dispersal from South American mainland
- Distinct races and species on different islands provide evidence of early stages of speciation

- Darwin spent only 5 weeks on the islands but his observations formed the foundation for his theory of evolution
- Now a UNESCO World Heritage site and ecotourism destination

Isabela:
- Prickly Pear cacti are first colonizers of volcanic landscapes
- Capable of long-distance dispersal by fleshy bird-dispersed fruits

Daphne Major:
- Site of 35-year study of natural selection in Galapagos finches
- Study by Peter & Rosemary Grant (Princeton)
- 14 Galapagos finches represent an **adaptive radiation**

Adaptive radiation:
- The evolution of ecological and phenotypic diversity within a rapidly multiplying lineage as a result of speciation
- From a single common ancestor the process results in an array of species that differ in traits allowing exploitation of a range of habitats and resources
- Four features commonly identify an adaptive radiation
  1. Recent common ancestry from a single species
  2. Phenotype-environment correlation
  3. Trait utility
  4. Rapid speciation

Galapagos island giant tortoise
- Largest tortoise in the world (880kg, 2m long), oldest living individual @ 170yrs
- Tortoises on different islands have different shell patterns
  - → 10 subspecies of a single species (*Geochelone nigra*) – endangered

Iguanas:
- Marine iguanas (*Amblyrhynchus cristatus*)
  - → Feed on seaweed
  - → Expels salt from nasal glands → salt-encrusted foreheads
- Terrestrial Iguana (*Conolophus subcristatus*)
  - → 80% of diet from prickly pear cactus

Birds:
- Loss of flight in cormorant
  - → Advantages for diving?
  - → Lack of predation?
- Sexually dimorphic Frigate bird

During the voyage of the H.M.S. Beagle (1831-1836)
- Heads west to **Australia** (2 months)

Australia
- Distinct flora and fauna with high levels of **endemism** and many unique adaptations
- Biological uniqueness due to long history of isolation from other land masses
- Although a continent Australia is also an island and shows many island characteristics e.g. endemism, radiations & unique adaptations

Endemism:
- Endemic species, which are restricted to a particular geographical region or habitat

Queensland
- Discovered Epiphytic fern

New South Wales
- Dry forests composed of Eucalyptus (Gum Tree)
  - → Dominant tree group in Australia

Koala
- Arboreal herbivorous marsupial
- Specialized diet of Eucalyptus leaves
- Can detoxify phenolics and terpenes in leaves

Rodent pollinated Banksia
- Plant is a shrub, but flowers are produced on the ground where rodents forage

Summary:
During the voyage of the H.M.S. Beagle (1831-1836)
- Lands in Brazil
  - → Notes high species diversity and novel adaptations
- Heads south to Patagonia
  - → Discovers strikingly different environments where abiotic factors dominate
- Heads west to Galápagos Islands (5 weeks)
  - → Evidence of early stages of speciation
  - → Spent only 5 weeks on the islands but his observations formed the foundation for his theory of evolution
- Heads west to Australia (2 months)
  - → Notes high endemism, novel adaptations and "biological uniqueness"
- Heads home to UK – Down house
  - → Gets married, has children, then starts work on assembling evidence for his evolutionary theory

<u>Reading Summary: Notes and quotes from Coyne - Chapter 4:</u>

Juan Fernández archipelago
- many edemic species found nowhere else in the world
- no species of amphibian, reptile or mammal
- gives evidence for evolution

Important questions regarding geographic distributions, now answered by "retrodiction" in light of evolutionary theory:
- Why did oceanic islands have such odd and unbalanced floras and faunas compared to continental assemblages?
- Why were Australia's native mammals marsupials, while placental mammals dominated the rest of the world?
- Why do distant areas with similar terrains and climates have species that appear similar, but are fundamentally different?
- These are the types of questions that plagued Darwin while on the voyage of the H.M.S. Beagle

Convergent evolution
- Species that live in similar habitats will experience similar selection pressures in their environment, will therefore evolve similar adaptations

Biogeographic patterns → Continental drift
- Marsupial fossils appear in Antarctica
- Freshwater frogs appear in eastern South America and subtropical Africa
- These observations can only be answered in light of biogeography and continental drift

- Biogeography makes predictions and solves puzzles

Continental islands vs. Oceanic islands:
- Continental islands were once connected to a continent but separated by flooding or moving continental plats
- Oceanic islands were never connected to a continent
- Disparity between types of plants and animals that appear on continental vs oceanic islands is hard to explain using creationist scenario

Oceanic islands:
- Mammals, amphibians, freshwater fish and reptiles often do very well when introduced to oceanic islands
- Displace and destroy native species: → Pigs and goats on Hawaii, Cane toad in Hawaii and Australia, Rabbits in Australia, etc.

Native to oceanic island	Missing from oceanic island
Plants	Land Mammals
Birds	Reptiles
Insects and other arthropods	Amphibians, Freshwater fish

- Oceanic islands have unbalanced biotas – missing major groups of organisms, and the same ones are missing on different islands
- Types of organisms there usually comprise similar species – a radiation – most often of which are types of species that can disperse most easily over large stretches of ocean
- Species that are most similar to those inhabiting oceanic islands are usually found on the nearest mainland even though habitats may be different
- When endemic species occur on oceanic islands, it can be explained by plant seeds hitching a ride on air currents, birds and bats flying, seals swimming and other animals hitching a ride on "rafts"

Continental Islands:
- "old" continental islands, such as New Zealand and Madagascar were isolated before many groups of species had evolved
- Had many ecological niches unfilled which opened the door for later-evolving species to successfully colonize and establish themselves
- Have a "somewhat" unbalanced flora and fauna
- Species on the islands closely resemble those found on nearest mainland

Envoi:
- Only evolution can explain the diversity of life that appears on islands
- Time and chance determine which species will end up on an island
- Because species on islands adapt to environments isolated from the diversity of species that live elsewhere, they are not good at co-existing with others

LECTURE 15: NEODARWINISM AND THE EVOLUTIONARY SIGNIFICANCE OF GENETIC VARIATION

1. Where does genetic variation come from?
2. How is it inherited?
3. How does it influence trait variation?
4. Why is genetic variation important for evolution?

Requirements for Darwin's theory:
- Genetics:
  - → **Variation** – Variation among individuals in a population
  - → **Heredity** – Progeny resemble their parents more than unrelated individuals
- **Selection** – some forms are better at surviving and breeding in a given environment
- Darwin had no understanding of genetics or the mechanism of inheritance

Genotype:
- **Genetic** constitution (makeup) of an organism
- Used in relation to a gene, or combination of genes
  - → Ex: Aa, AaBB

Phenotype:
- The trait of an organism as observed
- Used when discussing a trait or feature of an organism that varies
  - → Ex: The genotype AA or Aa lead to the phenotype of smooth skin while aa leads to wrinkled skin

Genome:
- The entire organism's DNA including **genes** and **non-coding** regions
  - → Genes – lead to phenotypes
  - → Non-coding regions – "Junk" DNA

What is a gene? – Various definitions
- The functional unit of inheritance
- A unit of hereditary information located on the chromosomes consisting of DNA
- A DNA sequence composed of **codons** essential for a specific biological function
  - → Codon: Sequence of 3 nucleotides (A,T,C,G) that code for an amino acid
    - → A sequence of codons make up the genetic code

Evolution requires genetic variation – where does it come from?
- Mutation
- Recombination
- Gene flow
- Hybridization

Independent assortment & **recombination**
- Independent assortment & recombination during meiosis generates enormous diversity
  - → Humans with **n**=23 chromosomes, 2^{23} = 8,388,608 possible gamete combinations
- Most genetic variability in a population results from sexual reproduction
  - → in any given generation input from mutation very small

Mutations
- Ultimate source of genetic variation
- Stable change in DNA sequence resulting in change of genotype
- Occurs at low and variable rate in all organisms
- Effects vary from neutral, deleterious, lethal or beneficial
  - → Fitness depends on environment in many cases

- Must occur in germ cells (sperm/eggs) – somatic mutations are not inherited
- Fruit fly:
  - → Wild type – "normal"
  - → Recessive mutant – no eye pigment
  - → Homeotic mutation – leg where antenna should be, severe, but not lethal
- Barbara McClintock (Cornell University, 1902-1992)
  - → Won 1983 Nobel prize for Physiology-Medicine
  - → Corn patterns didn't fit Mendellian ratios
  - → Discovery of "jumping genes" or transposable genetic elements in maize (corn)
    - → Arise by mutation and can move around the genome
- Mutant Australian daisy – potential outcomes
  - → Pollinators will avoid it because they don't recognize it – will disappear
  - → Pollinators may find it more appealing – will increase frequency in population
  - → May impact population via genetic drift
  - → May be a polymorphism → Both forms (White & Yellow) co-exist → Neutral
- Characteristics of mutation
  - → Unstoppable phenomenon
    - → Despite cellular mechanisms to correct errors during DNA replication
  - → Not directed by the organism or the environment
    - → Random with respect to effects on fitness
  - → Rates depends on the type of mutation → Also varies among genes
  - → Exposure to certain environmental conditions can affect mutation rate
    - → Mutagens, high temperature
- Mutation and the structure of DNA
  1. Point mutations
     AT**G**CAGT → AT**C**CAGT
  2. Insertions/deletions (including 'jumping genes') (Separated into potential codons)
     ATG|CAG|T → ATG|**G**CA|GT
     Results in **frame-shift** mutation – often deleterious, changing downstream codons
  3. Changes in repeat number (Separated into potential codons)
     ATG|ATG|ATG|ATG → ATG|ATG|**ATG**|ATG|ATG
  4. Chromosomal rearrangements
     ATGCAGT → TGACGTA

Motoo Kimura (1924-1994):
- Theoretical population geneticist was first to recognize the importance of neutral mutations

Mutation rates in eukaryotes	
Organism	**Number of fitness-affecting mutations per diploid genome each generation**
Drosophila (fruit fly)	1.2
Caenorhabditis (worm)	0.96
Arabidopsis (plant)	0.1-0.6
Mouse/Rat	0.91
Human/Chimpanzee	1.6-3

What about Humans?
- Each human carries 3-5 recessive lethal alleles
  → Alleles causing death when homozygous
  → Mating among relatives causes a higher incidence of offspring mortality

Inheritance and the transmission of genes among generations
- How is genetic information transmitted from parents to offspring
  → Mechanism of inheritance?
- How are traits expressed in parents and offspring
  → Is this influenced by how many genes control a trait?

Gregor Mendel (1822-1884)
- Priest and "father of modern genetics"
- Through controlled crosses with peas established the laws of inheritance
- Mendel's Laws re-discovered at the beginning of the 20th century by Hugo de Vries & Carl Correns

Design of Mendel's Experiment
- Cross between two pure-breeding lines of pea plants that differ in observable phenotypic trait
  → (Green parent) x (Yellow parent) → F1 self-crossed → F2
  → F1 = First generation; F2 = Second generation
- Expected results: Blending inheritance
  → When offspring of a cross show intermediate phenotype
  → (Green parent) x (Yellow parent) → Lime Green F1 Offspring → Lime Green F2 Offspring
- Observed results: Parental phenotypes retained -- (Y) = Yellow pea' (G) = Green pea
  → (G) x (Y) → F1: 100% (Y) offspring → F2: ¾ (Y) offspring, ¼ (G) offspring
  → Therefore: Yellow (Y) is **dominant**, Green (G) is **recessive**
  → 3:1 phenotypic ratio in F2 – ¾ dominant and ¼ recessive observed
  → 1:2:1 genotypic ratio in F2 – ¼ YY allele = (Y), ½ Yy allele = (Y), ¼ yy allele = (G)

Main conclusions from Mendel's experiments with peas
- Inheritance determined by discrete particles -- **genes** – "particulate inheritance"
- Most organisms carry **two** copies of each gene – **alleles** -- and are **diploid**
- Organisms produce **haploid** gametes (sperm, eggs) each containing **one** allele
- Offspring inherit one allele from each parent at random
- Dominant allele masks heterozygous allele in heterozygous genotype

Discrete vs. Continuous traits
- **Discrete** traits:
  → Simply inherited by 1 or 2 genes (major genes)
  → Mendelian genetics
  → 3 potential outcomes – **homozygous** dominant (AA), **heterozygous** (Aa), or homozygous recessive (aa)
- **Continuous** traits:
  → Complex inheritance by many genes (polygenes) of small effect
  → Quantitative inheritance
  → Continuum of outcomes – Ex: weight and height in humans
  → 65% of variation in human height is heritable

Genetic Polymorphism
- Different phenotypes exist in the same population of a species
- The occurrence of two or more discrete forms of a species in the same locality in such proportions that the rarest cannot be maintained by mutation alone
  → Usually means frequency of rarest mutation >5%

- Involves discrete phenotypes (called form or morphs) governed by segregation of a small number of alleles at 1-2 major genes
- Ex: sexual dimorphism, blood types

Gene number & phenotypic distribution
- Relation between number of genes controlling a trait and phenotypic variability
- Few genes – discontinuous (discrete) variation
- Many genes - continuous variation
  → Gene action is co-dominant
  → Heterozygote has an intermediate phenotype – dominance does not occur

Genetic analysis of variation
- Discontinuous variation - Mendelian genetics
  → Major genes, dominance and recessiveness, genetic polymorphism
- Continuous variation - Quantitative genetics
  → Polygenes, selection response, artificial selection experiments

Fisher's Fundamental Theorem of Natural Selection
- Sir Ronald A. Fisher (1890-1962)
- "The rate of increase in fitness of a population at any time is equal to its genetic variance in fitness at that time"

Reading Summary: Notes and quotes from Coyne - Chapter 5:

Hornets vs. Bees
- Hornets adapt to take over bee colonies
- Bees adapt unique defense to 'cook' scout hornet involving coordination
- Introduce European variety of bees, they get destroyed by hornets, as they are defenseless

Parasite/host adaptations & interactions
- Plants that look like insects
  → Chemicals & appearance → moths that want to mate end up spreading pollen
- Insects that look like plants
  → Avoidance of predators
- Darker soil → Darker mice; Lighter soil → lighter mice

Evolution & Selection
- "Mindless materialistic process that could achieve the same result as celestial design"
- Requires no will or conscious effort
- Population must be variable, variability must be heritable and any adaptations must increase potential to leave offspring
- Not all chance → "non-random survival of random variants"
- Selection cannot create a step that does not benefit its possessor

Reproduction, not survival, determines whether genes make it to next generation
- Same genes that increase ability to reproduce when you are young may cause enlarged prostate when old

Acacia → When one species does something to help another, it always helps itself in the process

Adaptations increase the fitness of the individual, not the species
- Never see adaptations that benefit the species at the cost of the individual
  → Male preying mantis & black widow spider?

Number of offspring is finite

- Allele frequencies in offspring may not be representative of parents
- Proportion of alleles can change by chance

Genes can become fixed in the population → rise to 100% frequency due to genetic drift

- A coin has a 50% chance of revealing a head or tail on a coin toss
- If you only have a few tosses, there is a high probability you will deviate from that 50/50 ratio

Small populations

- Proportion of alleles can change by chance
- Change in allele frequencies over time NOT due to natural selection
- Unusual blood type frequencies in Amish communities

Drift = random

- Can change allele frequencies no matter how useful they are
- Can overpower natural selection in small populations
- Sampling effect can be so large that it raises frequency of harmful genes even though selection works against them
- Even tiny advantages immeasurable by biologists can lead to important changes over time

Animal & Plant Breeding

- Domestic dog → from Eurasean grey wolf
- If fossils of dogs were to be discovered, they would be thought of as new species
- 150 breeds <10,000 years → Natural selection took 1000x longer to lead to the development of the grey wolf.
- Artificial selection → no bearing on fitness or reproductive success → completely manipulated
- Darwin → began the origin of species with notion of artificial selection because success of artificial selection is so obvious, that the logical leap from artificial to natural selection became natural

Evolution in the test tube

- Exposing captive populations to new environmental challenges
- Using microbes you can observe thousands of generations in real-time
  - → Genuine evolution → although challenge may be man-made
  - → More "natural" than artificial selection
- Lenski (See lecture 19)
  - → depleted then renewed glucose substrate of *E. coli*
  - → created a feast/famine environment
  - → now grow 70% faster than unselected strain
- If you remove a gene a microbe needs to survice, will the microbe evolve a way around the problem? Usually yes
- Barry Hall
  - → Deleted gene that creates lactase enzyme
  - → Grew bacteria on lactose substrate
  - → Eventually bacteria evolved workarounds to utilize lactose
- Natural selection can promote the evolution of complex, interconnected biochemical systems in which all parts are codependent
- Selection does not create new traits out of thin air – produces "new" adaptations by modifying preexisting features
- Paul Rainey
  - → Yielded a small-scale "adaptive radiation" of *Pseudomonas* under laboratory conditions

Resistance to Drugs and Poisons

- Given huge population sizes and short generation times, the chance of a mutation producing antibiotic resistance is high
- Best example we have of selection in action
- Creates an arms race between humans and microorganisms
- However, polio and measles have not evolved resistance to vaccines yet
  - → Theory of evolution doesn't predict that everything will evolve
- When a population encounters a stress that doesn't come from humans, such as a change in salinity, temperature, or rainfall, natural selection will often produce an adaptive response

Selection in the Wild

- Natural selection in the wild is incredibly slow
- Given the gradual pace of evolution it would be unreasonable to expect to see selection transforming one "type" of plant or animal into another – macroevolution, within a human lifetime
  - → We know that macroevolution happens, we just can't *see* it happening
- Medium ground finch of Galapagos
  - → Severe drought reduced supply of seeds on island of Daphne Major
  - → Finch was forced to turn to larger and harder seeds when small soft seeds ran out of supply
  - → Big-beaked individuals got food, survived, left more offspring
    - → Average beak size increased by 10% over the next generation
- Under prolonged drought, soils dry out quicker after the rains → Should produce seeds quicker
- Under normal conditions, it pays to delay seed production to grow larger and potentially grow more seeds
  - → Tested experimentally with wild mustard by Arthur Weis

Can selection build complexity?

- Complex features take a long time to develop
- It is reasonable to think that there are adaptations that could not have been built by selection, which would require thinking of another mechanism
- Advocates for intelligent design (ID) argue that complex mechanisms such as bacterial flagellum, blood clotting and the human brain must be due to ID as they defy Darwinian explanation → "god of the gaps"
  - → ID itself makes no testable scientific claims, but only offers half-baked criticisms of Darwinism
  - → We'll never be able to know how evolution created everything
  - → Science, like everything, has mysteries
- Clotting could have been built up in an adaptive way from simpler precursors
  - → Must have been an ancestral protein from which fibrinogen evolved
    - → Found likely precursor in sea cucumber
- "Ignorance more frequently begets confidence than does knowledge" – Charles Darwin
- Selection is perfectly adequate to explain changes that we see in the fossil record
- A span of ten million years is beyond our intuitive grasp
- Is natural selection sufficient to explain a really complex organ, such as the eye?
  - → Complex arrangement of the iris, lens, cornea; all of which must work together to create an image
    - → ID argument: Could not have been formed in gradual steps → how could "half an eye" be of any use?
  - → A possible sequence of events:
    - → Eyespots made of light-sensitive pigment, as seen in flatworms

- → Skin eventually folds in, which forms a cup that protects the eyespot and allows it to better localize the light source, as seen in limpets
  - → In abalones, part of the fluid in the eye has coagulated to form a lens
  - → Nearby muscles have been co-opted to move the lens and vary its focus
- → Dan-Eric Nilsson and Susanne Pelger of Lund University in Sweden
  - → Created a mathematical model starting with light-sensitive pigment
  - → Accepted "mutations" that improved visual acuity, rejected those that degraded it
  - → Through a series of 1,829 adaptive steps, their model yielded an eye, approximately 400,000 years using most conservative methods
  - → "It's obvious that the eye was never a real threat to Darwin's theory of evolution"
- Weak forces operating over long periods of time create large and dramatic change

LECTURE 16: MAINTENANCE AND MEASUREMENT OF GENETIC VARIATION

1. What processes influence the maintenance of genetic variation in populations?
2. How do we measure genetic variation and how much exists in populations?

Foundations of population genetics
- 1930-50 theoretical population genetics was initiated by Sir Ronald A. Fisher (1890-1962), J.B.S. Haldane (1882-1964) & S. Wright (1889-1998) and provided the foundations for "Neo-Darwinism" and the "New Synthesis"
- They showed that continuous variation and Darwinian natural selection were entirely consistent with Mendel's Laws
- They also demonstrated the evolutionary significance of genetic variation leading to several key questions and development of the field of ecological & evolutionary genetics

Key questions in ecological & evolutionary genetics
- What processes influence patterns of genetic diversity in natural populations?
- How much and what types of genetic variation occur in populations?
- How can we obtain empirical estimates of the amounts of variation in populations?

Important parameters used to measure patterns of genetic variation
- Polymorphism (P)
  - → Proportion of gene loci that are polymorphic
- Heterozygosity (H)
  - → Average frequency of heterozygous individuals per gene **locus**
  - → Locus: location on a chromosome that is usually a gene

Processes that influence patterns of genetic diversity
- Mutation (Increases genetic diversity)
  - → Ultimate source of genetic variation
  - → Caused by random errors during replication
  - → Can be any of the four types discussed in lecture 15
- Recombination (Increases genetic diversity)
  - → Introduces new combinations of mutations into a population
  - → No new mutations, just shuffling existing mutations
  - → Ex: mutations from one allele can recombine with another allele to create new combinations
- Random genetic drift (Reduces genetic diversity)
  - → Change in the frequency of a gene due to random sampling
  - → Variability gets lost
  - → Drift important when populations become small
- Natural selection (Can reduce or increase genetic diversity)
  - → **Purifying** (negative) selection → mutations that reduce fitness removed from population by selection
  - → **Positive** selection (adaptation) → mutations that increase fitness become fixed in the population
  - → **Balancing** selection → natural selection maintains diversity (heterozygote advantage)
    - → Polymorphism, can't fix a heterozygote
- Many controversies in evolutionary biology concern the relative importance of these forces in evolution

Diverse mechanisms maintain genetic variation within populations → Classes of explanations
- Mutation-selection balance

→ Less fit genotypes maintained by repeated mutation

- Different selective forces
  → Heterozygote advantage, frequency-dependent selection, fitness varies in space and time
- Variation selectively neutral
  → Alleles at polymorphic **loci** (plural form of locus) do not differ in fitness, hence none eliminated by selection

Artificial Selection

- Early evidence for the existence of genetic variation
  → Selection experiments on quantitative traits in different groups of organisms
  → Involves controlled breeding and selection of individuals for many generations
  → Ex: creation of dog breeds from wolf ancestor → goal of creating pet/working animal
- Selection response for bristle number in fruit flies - *Drosophila melanogaster*
  → Selection for high bristle number increases bristle number through generations
    → Implies variability within starting population
    → Top 5% of distribution
    → Relax after 20^{th} generation → Starts to level off
  → Control involves random mating → bristle number remains constant
- Selection response in maize
  → Shows that when you relax selection (high or low), levels return to normal over time
  → This type of artificial selection is the basis of plant breeding and is used to improve crop varieties
- Selection response in monkey flowers (John Kelly, U. of Kansas)
  → Artificial selection for large and small flowers in a wild population of monkey flowers with a normal distribution of flower size
  → Abundant quantitative genetic variation for flower size is maintained in natural populations
  → Striking floral variation within and between species of monkey flowers within a single population
  → A lot of quantitative genetic variability within populations
- Results of artificial selection experiments on quantitative traits
  → Selection responses demonstrate that abundant variation exists for polygenic (quantitative) traits
  → Provide no information on key population genetic parameters
    → Polymorphism or Heterozygosity
  → Comparative studies difficult as traits are often group specific

Two schools differ in prediction of amount of genetic variation that occurs in natural population (Values of P and H)

Classical school	Balance school
T.H. Morgan (1866-1945), H.J. Muller (1890-1967)	E.B. Ford (1901-1988), T. Dobzhansky (1900-1975)
Lab mutants	Natural populations
High homozygosity	Low homozygosity
Low polymorphism	High polymorphism
Wild type is best genotype Purifying selection reduces diversity	No best or ideal genotype Balancing selection favours diversity
$A^+A^+B^+B^+C^+C^+D^+D^+M^+M^+N^2N^+O^+O^+P^+P^+$	$A^3A^1B^2B^2C^2C^5D^4D^1M^1M^1N^7N^5O^3O^2P^1P^3$
Note: + = wild type, # = polymorphic allele	

Classical

- Wild type allele → Occasional new allele that become new wild-type
  → **Wild Type**: Fittest genotype
- Purifying selection removes "bad" alleles

Balance

- No fittest type – some organisms found all over the world
- Variability is important

Electrophoresis revolution (Richard C. Lewontin, Harvard University)

- **Allozyme** gel electrophoresis
  → Allozyme – different forms of the same protein
- Provided a way to ask - "what proportion of genes are variable (polymorphic)?"
  → Fundamental dispute between the classical and balance schools
- Initiated large scale surveys of electrophoretic variation in enzymes & proteins in diverse organisms and provided the first empirical evidence supporting the balance school
- Universal for any organism → All organisms have genes which make proteins and enzymes
- Visualize genetic variability
  → Homozygotes have stronger bands (F = Fast migrating, S = Slow migrating)
  → Heterozygotes – no dominance, can visualize both alleles
- Measuring diversity at genes controlling enzymes & proteins
- Monomorphic gene:
  → FF FF FF FF FF FF FF FF
- Polymorphic gene:
  → FF FS SS MM FM MS FF FS

Studies of enzyme polymorphism:

- Advantages
  → Many loci can be examined
  → Can be used in nearly any organism
  → Loci co-dominant, heterozygotes can be identified
  → Variation examined close to DNA level
  → Provides genetic marker loci for other studies
- Disadvantages
  → Variation is largely neutral or nearly neutral
    → Not under selection
  → Studies of quantitative inheritance are necessary to find out how much variation occurs for ecologically-relevant traits
    → Body size, fecundity and other life-history traits

Contrasting patterns of genetic diversity in generalist vs. specialist barnyard grasses

- Generalist – High diversity
- Specialist – Low diversity

Contrasting levels of polymorphism in plant species

- Polymorphisms compared in rare vs. widespread species
  → Higher polymorphisms in widespread species
  → Rare species have low genetic diversity
- Extinction
  → Low genetic variability
  → No habitat

DNA sequencing allows differences between individuals in single nucleotides to be identified

- SNP – single nucleotide polymorphism

- Can be measured for thousands of genes
- Can get measure of SNP frequencies → Measurements of polymorphism in DNA

DNA sequence variation among different organisms	
Organism	**DNA polymorphism**
Human	1/1000 bp
Rice	1/1000 bp
Mosquito	1/200 bp
Fruit fly	1/50 bp
E. coli	1/20 bp
Bp = Base pair	

Steven Wright (EEB)
- Found that domestication of maize from its progenitor teosinte caused 57% reduction in variation at SNPs
- Estimate that 1200 genes have been affected by artificial selection
- Domestication of crop reduced variability

Human genome project
- There is no single 'human genome'
- Individuals differ by thousands of SNPs in their genome sequence
- Today the genomes of >1000 prokaryotes and >100 eukaryote species have been sequenced

See Lecture 15 for Reading Summary: Notes and quotes from Coyne - Chapter 5:

LECTURE 17: ORGANISMAL REPRODUCTIVE DIVERSITY

1. Why did sex evolve?
2. How do we explain the diversity of reproductive systems?
3. What are the costs and benefits of inbreeding & outbreeding?

Reproductive Modes
- Asexual
- Sexual
  - Sexual System → Dioecious
    - → Hermaphrodite
      - Mating System → Cross-fertilization
        - → Self-fertilization

Darwin on sex
- "We do not even in the least know the final cause of sexuality ... why new beings should be produced by the union of the two sexual elements, instead of by a process of parthenogenesis... The whole subject is as yet hidden in darkness" (Darwin, 1862)

Water fleas (*Daphnia*)
- Different reproductive systems occur in different environments
- Cooler, calm water – Asexual
- Warmer, turbulent water – Sexual

Many perennial plants reproduce through sexual and clonal reproduction – Water Hyacinth
- Reproduces sexually over soil
- Clonally over water

Sex
- Costs
  - → Time and energy to find and attract mates
  - → Increased energetic costs
  - → Risk of predation & infection
  - → Cost of producing males
  - → 50% less genetic transmission
  - → Break up of adaptive genes combinations
- Benefits
  - → This is the big question – known as 'the paradox of sex'

Canadian researchers studying evolution of sex
- Sarah Otto (UBC), Aneil Agrawal (EEB, Toronto), Graham bell (McGill)

The two-fold cost of meiosis
- A sexual female contributes only 50% of her genes to the next generation compared with an asexual female
- This is known as a transmission bias favouring asexual

Hypothesis for the advantages of sex
- Bringing together favourable mutations – long term benefit
- Benefits of genetic variation in variable environments – short term benefit – "lottery model"
  - → Environment is a lottery → Better to buy more tickets, or photocopy a ticket multiple times?
  - → Variable offspring – some may be adapted to variable conditions
- Spatially heterogeneous environments 'Tangled Bank hypothesis'
  - → Environments themselves vary

- Temporally heterogeneous environments 'Red Queen hypothesis'
  - → Environments vary over time → Some organisms evolve faster than others
  - → Pests vs. Hosts
- Numerous theoretical models but a paucity of experimental evidence

Favourable combinations of mutations brought together more rapidly by sex
- Over time, large populations will more rapidly reach the "fittest" genotype
- Deleterious mutations are eliminated faster

Theory predicts spatial heterogeneity in selection can facilitate the evolution of sex
- No data to prove this until recently

Brachionus calyciflorus, a planktonic freshwater rotifer
- **Facultatively** sexual
  - → Can reproduce sexually or asexually
  - → Benefit to being able to do both
- Experiment by Lutz Becks and Aneil Agrawal (Nature, 2010)
  - → Placed in *B. calyciflorus* in 3 types of environments
    - → Homogeneous A, Homogeneous B, Heterogeneous AB
  - → Higher rates of sex maintained in populations evolving in heterogeneous habitats
  - → Over 12 weeks (~70 generations) → Experimental evolution
  - → Sex declined rapidly in homogenous environments
  - → Persisted at a much higher level with spatial heterogeneity
    - → Disadvantage to asexuality in variable environments

Evolutionary history of asexuality
- Asexuality (parthenogenesis) is sporadically distributed across the animal kingdom; more common in invertebrates but rare in vertebrates
- Asexuality (clonal propagation) is much more common in plants although few species (if any) are exclusively asexual
- Asexual species are usually at the tips of phylogenies; their long term evolutionary potential is probably low due to lack of genetic variation

Mystery of the Bdelloid rotifers - no sex for millions of years!
- A rare case of ancient asexuality in which males are unknown but diversification has led to > 300 spp.

Mating patterns – who mates with who and how often?
- Mates less closely related than random = Outbreeding
- Mates more closely related than random = Inbreeding
- In practice there is a continuum between outbreeding & inbreeding

The genetic consequences of inbreeding
- Genotypic frequencies changed
- Allele frequencies unchanged
- Heterozygosity reduced by 50% per generation with self-fertilization
- Homozygosity for deleterious recessive alleles results in inbreeding depression
- Frequency of alleles are unchanged → Combined in different genotypes

How do these two populations reproduce?
- Population 1 → FS FS FS FS FS FS FS FS
  - → Heterozygous → Fixed → Absense of homozygotes
  - → Asexual cloning population with heterozygous gene
- Population 2 → FF SS SS FF FF SS FF SS
  - → No heterozygotes
  - → High level of self-fertilization

- Using allozymes as genetic markers to study how populations reproduce

Heterozygosity in populations
- Heterozygosity decreases at different rates depending on mating patterns
  - → More related to self → Larger decrease in heterozygosity
- Heterozygosity decreases at different rates depending on population size
  - → Smaller population → Larger decrease in heterozygosity

Inbreeding depression
- The reduction in fitness of inbred offspring in comparison with outcrossed offspring
- Manifested by reductions in viability (survival) and fertility (reproductive output)
- Strong inbreeding depression favours survival of outbred offspring thus favouring outcrossed mating systems

Plants
- Darwin had a fascination with inbreeding & outbreeding plants
  - → A pioneer in inbreeding depression studies
- Most plants are hermaphroditic, containing both male & female parts
- Dioecy only occurs in 7% of flowering plants
  - → Sexual selection results in gender dimorphism
    - → Male → dispersing pollen → big flowers
    - → Female → making fruit

Evolution of selfing from outcrossing in annual Water Hyacinth
- Populations in Brazil are mostly outcrossing and visited by long-tongued bees
  - → (although selfing forms do occur)
  - → Larger flowers to attract bees
- Long-distance dispersal favours selfing forms
  - → A single individual can start a colony without mates or pollinators
    - → Known as 'Baker's Law'
  - → Jamaican and Cuban populations are largely selfing
    - → No pollinators on Caribbean islands

Automatic selection of a selfing gene (R.A. Fisher, 1941)		
	Outcrosser	Selfer
Seed	1	2
Pollen	1	1
Total Gene Copies	2	3
Selfing form has a transmission advantage – Mother and Father to its own seed Quantitative argument – Quality of offspring…?		

Reading Summary: Notes and quotes from Coyne - Chapter 6:

How sex drives evolution
- The peacock appears to violate every aspect of Darwinism
  - → Long tail produces aerodynamic problems in flight
  - → The sparkling colours attract predators
  - → A lot of metabolic energy is diverted to the tail which has to be regrown each year
  - → The question of how it came to be would plague Darwin
- Sexual dimorphisms
  - → Appear to violate evolutionary theory

→ Waste time, energy, and may actually reduce survival

The solutions

- If traits differ between males and females of a species, the elaborate behaviours, structures and ornaments are nearly always restricted to males
- The currency of selection is not really survival
  - → Successful reproduction
- Sexual selection comes in two forms
  - → Direct competition between males
    - → Males battle each other
    - → Males battle to control territory
  - → Female choosiness
    - → Indirect competition between males
    - → Ex: African long-tailed widowbird
      - → Experiments conducted where males with clipped tails, normal tails and elongated tails were allowed to mate
      - → Males with artificially long tails gained an increase in matings
        - → If males with unnaturally long tails won more females, why haven't longer tails evolved?
        - → Likely because having tails that long would reduce longevity more than they would increase ability to get mates
      - → Malte Andersson describes 232 experiments in 186 species showing that a huge variety of male traits are correlated with mating success involving female choice

Why sex?

- Why sex evolved is one of evolution's greatest mysteries
- Any individual involved in the act is sacrificing 50% of their genetic contribution to the next generation
- Why hasn't the cost of sex led to its replacement by Partenogenesis – development of eggs without fertilization?
  - → Sex must have some sort of evolutionary advantage that outweighs the cost
  - → Several theories exist that offer explanations
- Why are there only two sexes that mate and combine gametes?
  - → Two is the most robust and stable
- Why do two sexes have different numbers and sizes of gametes?
  - → Presumably evolved from a condition where gametes were of equal size
  - → Record number of children produced by a woman: 69
  - → Record number of children produced by a man: ~1000
- Differential investment
  - → Investment in expensive eggs which are limited in number
  - → Investment in pregnancy
  - → Because of their investment, it is in their best interest to be picky rather than promiscuous
  - → Only 2% of animal species are monogamous
    - → Male sticks around to take care of offspring
- Explanations for sexual dimorphism that don't involve sexual selection
  - → Some females are larger because they produce larger gametes
  - →

Breaking the Rules

- Sexual dimorphisms occur in "socially monogamous" species
- Males aren't competing for females, why evolve bright colours and ornaments?
  - → Appearances are deceiving
  - → Appear monogamous, not actually monogamous
- Species showing little dimorphism in behavior and appearance tend to be truly monogamous
  - → Geese, penguins, pigeons, parrots
- In some species where males carry brood pouches, males tend to invest more in offspring than females
  - → Reproductive strategy reversed
    - → Females compete for non-pregnant males, colourful and showy
  - → Seahorses, pipefish and phalaropes are the exceptions that prove the rule
  - → Their "reverse" decoration is what one would expect if the evolutionary explanation of sexual dimorphism is true
  - → Wouldn't make sense if these species were "created"

Why Choose?

- What benefit does a female have by choosing a particular mate?
  - → Directly – by picking a mate that will help her produce more, or healthier young during the act of child care
    - → Choosing males with better territories
  - → Indirectly – by choosing a mate with better genes than those of other males
    - → Red colour in finches come from carotenoid pigments in seeds they eat
    - → Colour preference may be linked to diet and health
    - → Male gray tree frogs with longer calls produce tadpoles that grew faster and survived better
- Evolutionary theory shows that three types of genes will increase in frequency together
  - → Genes for a male "indicator" trait reflecting good genes
  - → Genes that make a female prefer that indicator trait
  - → The "good" genes reflected by the indicator
- Sensory-bias model
  - → Evolution of sexual dimorphism driven by preexisting bias in female's nervous system
  - → Bias can be by-product of natural selection from function other than mate selection, such as finding food
  - → If there was a preference for the colour red because it helped them locate ripe fruits and a mutant male appeared with red patch, he might be preferred due to the favourable colour
  - → Females may simply like novel features
    - → Females derive neither direct nor indirect benefits from choosing a particular mate
  - → Experiments with several species show that females have preference for traits for which they have never been exposed

LECTURE 18: POPULATION STRUCTURE, GENE FLOW AND GENETIC DRIFT

1. Geographical variation and the genetic differentiation of populations
2. Gene flow – the movement of genes across the landscape
3. Genetic drift and other **stochastic** forces

Stochastic – random forces

The Fisher-Wright debate
- Wright saw an important role for population structure and genetic drift in evolution
- Fisher disagreed and argued that most evolution occurred in large populations by natural selection
- Continues to be a debate

North- versus south-facing slopes have different microclimates
- Habitats very close together
- South facing slope heats up faster in spring → Genetic differentiation

Population
- A group of individuals of a single species occupying a given area at the same time
- Mark-recapture studies to estimate population sizes of mobile organisms
- Population size is difficult to estimate

Migration
- The movement of individuals from one population to another
- Ecological phenomenon

Gene flow
- The movement of genes from one population to another
- Genetic phenomenon

Variation within populations
- How much of the observed variation among individuals is genetic in origin?
  - → Heritable variation
- Does the variation contribute to fitness differences among individuals?
- What about variation among populations?
  - → Analysis of variance → How much variation is within group vs. between groups?
  - → Ex: Humans – More variation within racial groups than between racial groups (Ex: Skin colour has small numbers of loci)

Geographic differentiation
- What proportion of all genetic variation in a species is due to differences between populations?
  - → How is diversity distributed within vs. between populations?
- Are some loci or traits more differentiated than the genome-wide average?
  - → Population differentiation due to local adaptation?

Effects of selection, gene flow & genetic drift on population divergence
- Two populations from same origin
- Natural selection drives them apart due to differing geographical environments
- Genetic drift
  - → Random process by which genes become different in small population, irrespective of fitness
  - → Loss in rare alleles
- Gene flow
  - → Acts as cohesive force to keep populations from pulling apart

Gene flow
- Difficult to observe and measure
- Distinguish potential (migration) vs. actual
- Distinguish gamete vs. individual
  - → Different genetic impacts
- Use experimental approaches
- Use neutral genetic markers
  - → Polymorphic neutral genetic variation used to study population processes affecting genetic diversity
  - → Can count genotypes on a gel

Two populations fixed for alternative alleles
- Two populations homozygous but for alternative alleles
- How much gene flow occurs between them?
- (FF FF FF FF) ⇆ (SS SS SS SS)
  - → Collect offspring over time
  - → Score heterozygotes FS in offspring
  - → Frequency of heterozygotes = estimate of gene flow
  - → May be asymmetric → gametes moving downstream of a river

Genetically-modified organism (GMO)
- Concern
  - → Anti-multinational corporation
  - → Health concerns -- frankenfoods
  - → Scientists plating god -- Naturalist fallacy – Horizontal gene transfer
  - → Biodiversity issues
- Canola
  - → Measuring gene flow – an example from modern agriculture
  - → Escape of **transgenes** into wild relatives by gene flow
    - → Transgene = gene transfer using recombinant DNA technology
  - → Many crops have close relatives with which they are inter-fertile
    - → Rice, oats, canola, carrots
  - → Hybridization between crops and related weeds is well documented
  - → Gene flow between crop and weed sunflowers
    - → Most gene flow occurs over a short distance, but a small amount occurs as far as 1km
  - → Escape of crop transgenes into wild relatives by gene flow
  - → Risk assessment - Isolation distance
    - → Proximity of wild (weed) relatives
    - → Pollination system – wind vs. animal
    - → Mating system – selfer vs. outcrosser
  - → High risk: Wind pollinated outcrosser with relatives nearby
  - → Low risk: Selfer with no relatives nearby
  - → Corn: in Mexico, wild teosinte populations are contaminated with GMO alleles

Random
- Stochastic (unpredictable or random) evolutionary forces:
  - → Mutation
  - → Recombination
  - → Gene flow
  - → Genetic drift

- Deterministic (predictable or non-random) evolutionary force:
    - → Natural selection
- Stochastic processes resulting in a loss of diversity
    - → Genetic drift: stochastic changes in allele frequency due to random variation in fecundity & mortality; most important when populations are small
    - → Population bottlenecks: a single sharp reduction in numbers causing a loss of diversity
    - → Founder events: colonization by a few individuals that start a new population with only limited diversity compared with the source population
- Random fluctuations in allele frequencies in populations of different size
    - → Genetic drift is more evident in small populations
    - → Movement of alleles overall
    - → Rare alleles lost in small populations
- Founder events and population bottlenecks can reduce population to a single allele

Can genetic drift be important for adaptation?
- Controversial issue
- Drift often requires certain conditions to occur
- The role of genetic drift in the evolution of selfing in annual water hyacinth
    - → Theoretical models and field studies in Brazil, Jamaica & Cuba to test the models

Tristyly – a plant sexual polymorphism
- Genetic polymorphism with phenotypic expression
    - → Symmetrical mating system
    - → Disassortative mating, between unlike phenotypes
        - → No selfing
    - → Governed by two diallelic loci (S,M) with epistasis between S and M
        - → Epistasis:
            - → interaction between alleles at different loci affecting phenotype
            - → One allele affects and overrides other allele
- Three morphs
    - → Rare morph enjoys fitness advantage
    - → 1:1:1 morph frequencies at equilibrium
    - → Genetic drift will affect morph
        - → Do you lose morphs equally?
        - → S-allele is at lowest frequency → Lost first → Becomes dimorphic
        - → Inbreeding begins to occur – Homozygosity → M-allele is next to disappear
    - → Genetic polymorphism → genetic monomorphism
    - → Natural selection begins selecting those that self
- Polymorphism maintained by frequency-dependent selection

LECTURE 19: NATURAL SELECTION AND ADAPTATION

1. Types of selection
2. Determining the mechanisms of selection
3. Evolution by pollution
4. Experimental evolution

Orchid from Madagascar with long floral tube pollinated by night-flying moth with exceptionally long proboscis
- Darwin predicted the existence of the moth
- A century later it was discovered
- Example of co-adaptation

Fitness:
- Relative genetic contribution of individuals to next generation as a result of differences in viability and fertility (= Darwinian fitness)

Selective advantage:
- Some individuals better adapted to the environment and thus have higher fitness

Adaptation:
- Noun -- Any trait that contributes to fitness by making an organism better able to survive or reproduce in a given environment
- Verb -- The evolutionary process that leads to the origin and maintenance of such traits

Artificial selection
- Domesticated plant and animals
    - → Selection experiments in genetics
- Selection by humans
- Has a purpose or goal

Natural selection
- All organisms
- Selection by abiotic & biotic environment
- No purpose or goal
    - → Simply a blind mechanistic process with no foresight
    - → Note: Random
    - → Compare to Lamark's (incorrect) view → Giraffe's goal was to reach higher leaves

Phenotypic traits and distributions

Continuous distributions
- Normal distribution with mean & standard deviations
- Typical with size or number traits
- Example of quantitative inheritance

Stabilizing selection
- Favoured traits are close to the population mean (average)
- Leads to a narrower peak distribution
- Ex: Human birth weight
    - → Very small and very large babies have higher mortality rates

Directional selection
- Favoured traits favour one extreme, either right or left of the mean
- Leads to a skew, either right or left of the mean
- Ex: Beak size in Galapagos finches
    - → As seed abundance decreased, the population fell

→ As seeds became harder, average beak size increased

Disruptive selection

- Favours both extremes
- Leads to a shallower, or twin-peak distribution
- Leads to character divergence and sometimes speciation
- Requires spatial heterogeneity or discrete resources
- Ex: Beak size in African finches
  - → Beaks of one group became smaller, adapting for soft seeds
  - → Beaks of another group became larger, adapting for hard seeds

The struggle to determine the mechanisms of selection

- Today hundreds of measurements of selection demonstrating fitness differences & evolutionary change in traits
- Fewer convincing cases that demonstrate the mechanisms (agents) of selection in natural populations – ecology is difficult!

Evolution of cyanide resistance - scale insects

- Alleles conferring cyanide resistance are originally found at low frequency in populations
- Resistance spreads through the population when selection is imposed by cyanide fumigation
  - → Resistant individuals have higher reproductive success
- This process serves as model for the evolution of many forms of resistance e.g. antibiotics, insecticides, herbicides

Evolution by pollution

- Evolution of heavy-metal tolerance in grass species
- Evolution of industrial melanism in the peppered moth
- The peppered moth (*Biston betularia*) and industrial melanism
  - → Light and dark forms of species that rest on trees
  - → In UK, before 1850 dark moths rare; caused by single dominant allele
  - → Industrial pollution blackened tree trunks near cities resulting in increase in black form
  - → Black variant replaces white in polluted areas; white form predominates in rural unpolluted areas
  - → Mechanism of selection thought to be predation by birds and differences in crypsis (camouflage) depending on the background of tree trunks
- H.B.D. Kettlewell (1907-1979) – His triumph
  - → E.B. Ford recruits Kettlewell to Oxford to investigate the bird predation hypothesis
  - → Observations and experiments in the 1950s involving mark and recapture of moths provide support for the hypothesis
  - → His findings thought to provide the first demonstration of the mechanism of natural selection in the wild and now feature in most biology textbooks and museums
- Doubts raised about Kettlewell's bird predation experiments
  - → Michael Majerus (Cambridge) and Jerry Coyne (Chicago)
  - → Moths raised in the lab and this may have influenced behaviour
  - → Moths put on trunks at unnaturally high densities
  - → Moths rarely seen on trunks
  - → Releases conducted during the day
  - → Possibility of bat predation not investigated
- Decline in frequency of the black (melanic) form after introduction of the 'Clean Air Act' in the UK in 1956

  - → Lag in evolutionary responses to changes in air pollution levels reflects the time required for forests to return to a more unpolluted state as well as a low initial frequency of the recessive allele for typical coloration
- Mouse coat colour polymorphism in contrasting habitats maintained by avian predators
  - → Hopi Hoekstra (Harvard)
  - → Light-coloured (agouti) mice fare better in light-coloured or sandy environments than dark mice
  - → Dark mice fare better in dark soils than light-coloured mice
- Evolution of heavy metal tolerance in plants
  - → A.D. Bradshaw (U. of Liverpool)
  - → Mine waste heavily polluted with heavy metals
    - → Ex: lead, copper, nickel)
  - → Most mines less than 100 years old
  - → Heavy metal tolerant genotypes occur at very low frequency in nearby uncontaminated pastures
  - → Tolerant genotypes invade mine tailings from nearby pastures
  - → Gene flow between pasture and mine restricted because of flowering time differences between mine & pasture
  - → Genes for tolerance maintained on mines
  - → Heavy metal tolerance in plants has evolved independently in many geographical areas including Ontario, Canada
    - → Tufted hairgrass at Sudbury mines
- Evolution of zinc tolerance in grasses
  - → Why don't tolerance genes spread in the pasture?
    - → No adaptive significance to have the genes spread (no positive selection)
    - → Cost to tolerance → physiological machinery to detoxify metals is physiologically demanding

Evolution in the lab – 'experimental evolution'

- Richard Lenski (U. of Michigan)
  - → Founder of 'experimental evolution'
  - → 20 yr experiment with *E. coli*
  - → 40,000 generations of evolution
- Single strain
  - → Twelve populations propagated under minimal glucose/citrate medium
  - → 42,000 generations in serial culture
- Relative fitness over time
  - → Samples frozen at intervals allowing relative fitness of different generations to be compared
  - → All populations rapidly increased in fitness
  - → Similar adaptations across strains (e.g. larger cell sizes, higher maximal growth rates on glucose)
  - → Parallel mutations at same genes
  - → Some unique adaptations and distinct genetic changes
  - → Novel key innovation in single strain after 33,000 generations

Open questions about adaptation

- What is the relative importance of standing genetic variation (variation already present in a population) vs. new mutations?
- Are convergent adaptations in unrelated organisms the result of the same or different genes?

See Lecture 15 for Reading Summary: Notes and quotes from Coyne - Chapter 5:

LECTURE 20: SPECIES, SPECIATION AND HYBRIDIZATION

1. What is a species?
2. Evolution of reproductive isolation
3. Modes of speciation
4. Adaptation & speciation
5. Evolutionary significance of hybridization

Hawaiian honeycreepers have all descended from a single species of finch in the last 10 million years
- How did this occur?

Species
- "Individuals closely resembling each other" – Darwin, 1859
- "When we understand the origin of reproductive isolating factors, we understand the origin of species" - Coyne 1992

Speciation - Key questions
- What ecological and genetic conditions are required for speciation to occur?
- How does reproductive isolation evolve?
- How many genes are involved?
    - → Speciation genetics
- Is the evolution of adaptation required for speciation?
- Many definitions of "Species"

Two main species concepts of Species

Taxonomic (or morphological)
- Based primarily on distinct morphological differences
    - → Certain level of arbitrary-ness to it
    - → How do you draw the line between two different species?

Biological
- Based on inter-fertility (crossability) among individuals
- Able to produce fertile offspring between two individuals
- Under some conditions it's impossible to investigate inter-fertility, so taxonomic concept has to be used sometimes

Concepts vary among different groups of organisms – no universal concept

Ernst Mayr (Harvard University, 1904-2005) – The biological species concept (1942)
- "a group of interbreeding natural populations that are reproductively isolated from other such groups"
- * Although Mayr first formally defined the BSC, Dobzhansky first suggested the idea

Two main modes of speciation
- Allopatric
    - → Means "growing apart"
    - → Single population becomes subdivided due to barrier
        - → Dispersal event → Geographical isolation
        - → Limits opportunities for gene flow
    - → Populations diverge overtime
        - → Differences in polymorphic and monomorphic loci
        - → Alternate alleles get fixed in either populations

        - → Become different genetically
    - → If they come back into contact
        - → Secondary contact
        - → Cannot then interbreed
    - → Most common form of speciation
- Sympatric
    - → Means "growing together"
    - → Rare form of speciation
    - → Subpopulation diverges
        - → Gene flow is truncated to allow a subpopulation to achieve reproductive isolation
    - → Common in plants

Reproductive isolation (RI) -- **Stages** when **RI** can occur:
- Helps determine genetic basis

Reproductive isolating mechanisms		
Speciation involves the evolution of reproductive isolation between populations		
Finding a compatible mate ↓	Geographical, Ecological	Premating isolation ↓ Preventing zygote formation
Mating & fertilization ↓	Temporal, behavioural, Mechanical, Prevention of gamete fusion	
Development of zygote ↓	Abnormal development of hybrids	Postmating isolation ↓ Preventing proper functioning of zygotes once they are formed F_2 breakdown Intrinsic vs. Extrinsic
Adult growth & survival ↓	Inviability	
Reproduction & fertility of offspring	Sterility	

Premating isolation in apple maggot flies (*Rhagoletis pomonella*): habitat and temporal isolation
- Species was restricted to hawthorns
- Arrival of domesticated apples in 19^{th} century led to host shift
    - → Sympatric speciation
    - → Genetically based host-shift
- Differences in host plant emergence and mating on preferred host restricts hybridization
- Reduces gene flow in sympatry (same region) to ≈ 6%

Premating isolation in species of monkey flower: pollinator preferences & altitude
- *Mimulus lewisii* – Bumblebee; *Mimulus cardinalis* - Hummingbird
- Isolated due to different pollinators and occurrence in different environment
- Different "species" – but can be hybridized
    - → Not a lot of genetic differences
- The two parental species are inter-fertile and produce fertile F2 plants displaying a wide range of character combinations
- However, hybrids are rarely seen in the field because of elevational separation & pollinator preferences

Postmating Isolation
- In some cases, reproductive isolation occurs in F_2

→ Cotton plants
- Intrinsic factors
    → Genetic – problem with the organism itself
    → Sterility or lethality of F_2 offspring

Relation between **genetic distance** and postmating (zygotic) isolation in fruit flies (Coyne & Orr, 1997)
- Genetic distance - A measure of the degree of genetic differentiation between samples
- Take pairs of *Drosophila* species as test organisms
    → Relationship between postzygotic isolation and genetic divergence
    → As organisms diverge – less likely to produce fertile offspring
- The more genetically differentiated pairs of flies are
    → More likely to be reproductively isolated
- The plot can be viewed as a time course for the evolution of reproductive isolation

Mule
- Hybrid offspring of cross between male donkey and female horse
- Produces sterile gametes

Crow species in Europe – an example of extrinsic postzygotic isolation due to poorly adapted hybrids
- Two species meet along a "contact zone"
- Hybrids have low fitness due to extrinsic (environmental) factors
    → Gene flow is not pervasive → Allopatric
- Each separate species has adapted to its own environment, hybrids do not do well in either

Is the evolution of adaptation required for speciation?
- In many cases, the evolution of local adaptation is a result of divergent selection
    → Reproductive isolation and speciation
    → Commonly referred to as 'ecological speciation' and
    → Current research focuses on determining the mechanism of selection and identifying 'speciation genes'
- Evidence of adaptation to different environments in various species

Adaptation to freshwater in 3-spined stickleback involves loss of bony defensive armour
- Eda - a key gene for understanding adaptation and speciation during colonization of freshwater lakes from marine environments
- Species differ because of the ecology of different environments
- Marine: Bony armour protects against large fish predation, sea doesn't freeze in winter
- Freshwater: loss of plates increases growth rate helps fish to survive winter and breed earlier
    → Production of plates is costly, lakes freeze in winter
    → Breed early and develop faster to have a better chance at survival

Adaptive radiation
- The evolution of ecological and phenotypic diversity within a rapidly multiplying lineage as a result of speciation
- From a single common ancestor the process results in an array of species that differ in traits allowing exploitation of a range of habitats and resources
- Four features commonly identify an adaptive radiation
    1. Recent common ancestry from a single species
    2. Phenotype-environment correlation
    3. Trait utility
    4. Rapid speciation

What causes adaptive radiations?
- Ecological opportunity

→ Abundant resources and few competitors on oceanic islands or their aquatic counterparts e.g. African rift lakes
→ Extrinsic factor
- High rates of speciation characterize the clade
    → **Clade**: Branch on the "tree of life" or phylogenetic tree
        → Group that consists of ancestor and its descendants
    → Intrinsic – some species can speciate faster
    → Can be tested by comparing with mainland clade
    → Darwin's finches & Hawaiian honeycreepers also radiated on mainland (although not as much)
    → Galápagos mockingbirds have not radiated on islands or continents
        → Fairly specialized in resource use?
        → Limited in genetic variability?
- Origin of a key innovation
    → Interaction between organism and environment
        → Exploits a new set of resources and adaptive zone
    → Ex: toepad in Anoles; floral nectar spur in Columbines, flight in birds

Adaptive radiation of beak morphology in Hawaiian honey creepers
- How much variation is there in beak morphology comparing honey creepers with other bird groups?
- Variation worldwide in passerine beak morphology
- Hawaiian honey creepers have enormous diversity given number of species in lineage

Hybridization
- The exchange of genes between species as a result of occasional inter-specific mating
- Varies among different groups of organisms
    → Common in plants and fish, rare in mammals
- Can result in complex patterns of variation
- Variation can be of evolutionary significance resulting in speciation, especially by polyploidy

Polyploidy
- An organism, tissue, or cell with more than two complete sets of homologous chromosomes
    → Diploid gametes fusing with haploid gametes → triploid zygote
    → Fusion of two diploids → tetraploid
        → Balanced (even) chromosome numbers → fertile
        → Odd chromosome numbers → infertile
- Polyploid conditions range
    → Autopolyploidy
        → Single population produces polyploid individual
        → (AA + AA) → AAAA
    → Allopolyploidy
        → Hybridization between two species
        → Most common type of polyploidy
        → Tetraploid forms by unreduced gametes in meiosis
            → (AA + BB) → AABB

Evolutionary significance of polyploidy
- Polyploids reproductively isolated from their diploid parents hence a form of sympatric speciation
- Polyploids exhibit novel phenotypes allowing exploitation of new habitats
    → Versatile

- Hybrid vigour evident due to heterozygosity, particularly in allopolyploids
  - → Genetic benefit of multiple chromosomes
- Approximately half of all flowering plants are of polyploid origin including many crop plants & invasive species

Reading Summary: Notes and quotes from Coyne - Chapter 7:

The Origin of Species

- Ernst Mayr totaled up the names of bird specimens he found on his expedition and counted 136 as named by natives
- Western zoologists using traditional methods recognized 137 species
- Both locals and scientists distinguished the very same species of birds living in the wild
- Discontinuities of nature are not arbitrary, but an objective fact
- Discrete clusters are known as *species*
- Although being titled "the origin of species," the book had little to say about the subject and would have been more appropriately titled "The origin of adaptations'
- Biologists struggled to explain how a continuous process of evolution produced discrete groups known as species
- At what point are differences in populations large enough to make us call them different species?
- The concept makes the designation an arbitrary exercise but species have an objective reality
- Some animals coexist in the same location but never exchange genes
  - → Reproductively isolated from one another
- Species are not distinct because they look different – there are also barriers that keep them from interbreeding
- Biological Species Concept
  - → A group of inter-breeding natural populations that are reproductively isolated from other such groups
  - → Takes care of many problems that appearance-based concepts can't handle
  - → Inuit and !Kung may not mate directly, but there is *potential* gene flow despite their difference in appearance
  - → Cannot be applied to extinct organisms
- Two species of monkey flower, *Mimulus,* live in the same area but rarely interbreed because they are pollinated by different organisms
- Divergent selection – selection that drives different populations in different evolutionary directions
  - → Languages can diverge in isolated populations
  - → Languages change more rapidly when there is less mixing of individuals
  - → Languages are like species in that they occur in discrete groups rather than in a continuum
- Sterility and inviability of hybrids
  - → By-products of genetic divergence caused by natural selection or genetic drift
  - → Genomes can become so different that they no longer work well together
- Species don't arise because there are empty niches in nature
- Species are evolutionary accidents
- Speciation depends largely on geographical isolation
  - → Might simply become separated by accidental long distance dispersal

  - → If populations must be physically isolated then we should find the most recently formed species in different but nearby areas
  - → Geographic speciation should still be occurring
    - → Orchid *Satyrium hallackii*
    - → "Evolved" shorter tubes in coastal regions to attract bees rather than hawkmoths
  - → Reproductive isolation between two physically separated populations should increase over time
- Process occurs too slowly for us to see them in real-time
  - → Can take snapshots of the process at different evolutionary stages and putting them together in a conceptual movie
- New species can arise without the need for geographic separation
  - → Sympatric speciation
  - → Hard to split one gene pool into two while everyone remains in the same area
  - → If you can find several species in a small area it maybe good evidence to support this theory
  - → Allopolyploid speciation
    - → Starts with hybridization of two different species living in the same area
    - → Requires that they have different numbers or types of chromosomes
    - → Doesn't undergo chromosome pairing
    - → Technically a new species, as it can no longer mate with either of the parent species
  - → Autopolyploid speciation
    - → Doubling of all the chromosomes of a single species
  - → Need a rare event in two successive generations
    - → Formation and union of sperm and eggs with unusually high chromosome numbers
  - → Single parent can produce millions of eggs and pollen grains, so a rare event becomes statistically less rare
- Red viscacha rat of Argentina
  - → Has 112 chromosomes
- Polyploid speciation differs because it involves changes in chromosome number rather than genes
- Also much faster

LECTURE 21: PHYLOGENETICS AND MACROEVOLUTION

1. How best to classify life – systematics, taxonomy, and cladistics
2. Phylogenetic trees and the reconstruction of evolutionary history using molecular data
3. Character evolution, the origin of adaptations and key innovations

Carolus Linnaeus (1707-1778)
- The "father" of taxonomy
- Binomial nomenclature
- Hierarchical system of classification
- Kingdoms → Phyla → Classes → Orders → Families → Genera (Genus) → Species
  - → Memory triggers to remember order: http://www.mnemonic-device.com/biology/
  - → **K**evin **P**lease **C**ome **O**ver **F**or **G**reat **s**andwiches
  - → **K**ing **P**hilip **C**ame **O**ver **F**rom **G**reat **s**pain

What is the purpose of a biological classification?
- Name is a key to the literature on an organism → Therefore has predictive power
- Enables interpretation of origins and evolutionary history

Taxonomy
- The theory and practice of classification
  - → Taxon -- A taxonomic unit at any level
  - → Taxa – Plural for taxon
  - → Taxonomic units: K P C O F G s

Systematics
- The study of biodiversity and the evolutionary relationships among organisms
  - → Relationships visualized as evolutionary trees

Schools of Taxonomy: Philosophical wars of the 70s & 80s
- Phenetics
  - → Classifying species based solely on overall resemblance. Now largely dead!
  - → Negates homoplasy and convergent evolution and ancestral traits
- Cladistics
  - → Classifying species on the basis of their phylogenetic relationships

The birth of cladistics and the building of phylogenetic trees (Will Hennig, 1913-1976)
- phylogenetic trees provide a depiction of the evolutionary relationships among groups of organisms – important to appreciate they are an hypothesis about evolutionary history

Phylogenetic trees
- Contain branches much like a tree
- Nodes
  - → Speciation events
  - → Common ancestors

Monophyletic group → A single ancestor gave rise to all species in that taxon
Non-monophyletic group → A taxon whose members are derived from two or more ancestral forms
Reconstruction of phylogenetic history:
- Identification of ancestral and derived traits
- Ancestral trait = A trait shared with a common ancestor
- Derived trait = A trait that differs from the ancestral trait in a lineage

Homology
- Similarity of traits due to shared ancestry
- Human and fish skeleton are homologous

Homoplasy
- Similarity of traits as a result of convergent evolution
- Convergent evolution:
  - → Evolution of structures that resemble one another and perform similar functional roles
  - → Shared ecology of unrelated organisms
  - → Ex: Succulence and spiny growth in desert environments
  - → Ex: Independent evolutionary radiations of cichlid fishes in African lakes (Malawi, Tanganyika)
    - → The similarity in form indicates convergence in feeding strategies

Relevance of molecular biology to evolution & phylogeny reconstruction
- All life is related through branching descent
- Common genetic code is evidence that all life is related
- Evolutionary relationships among species are reflected in their DNA and proteins

Inferring species relationships from nucleotide sequences
- Genes or parts of a gene can be sequenced for different species
- Species can be assessed for changes in the sequence of nucleotides
- These changes can be used to construct relationships in a branching diagram (phylogeny)

DNA sequencing is enabling rapid construction of the tree of life
Using phylogenies to understand the origin and evolution of traits – Key innovations:
- Origin of a novel trait resulting in adaptive radiation
- Carriers of the trait can exploit new resources or sets of habitats
- Usually associated with rapid evolutionary diversification (e.g. adaptive radiations)

Key trait associated with increased diversification rate
- Low diversity clades have less branches, few innovations
- Key innovations lead to high diversity clades
  - → **Key innovation**: Origin in a novel trait resulting in an adaptive radiation to exploit new resources or habitats previously unavailable prior to trait acquisition
- Ex: Evolution of flight
- Ex: Adaptive radiation for pollinators in columbines associated with origin of nectar spur
  - → (Scott Hodges, UCSB -- PNAS, 1994)
  - → Columbines have long tubes (spurs) containing nectar
    - → Display diverse flowers associated with different pollinators
    - → Red flowers → Bird pollinators
  - → Phylogeny shows rapid burst of speciation with acquisition of nectar spur
    - → Short clade-branch lengths in comparison with sister group
    - → Explosive adaptive radiation -- 16 fold variation in nectar spur length among species associated with 7 independent pollinator shifts
      - → 2 from bee to bird, 5 from bird to hawkmoth
    - → Ancestor evolved from bee pollination to hummingbird to hawkmoth
      - → Increasing spur length, adapting to different pollinators with different (longer) spur length
      - → Clear directionality with no evidence of reversal to shorter spurs
    - → Acts as a premating isolation mechanism → Speciation event → Leads to pollinator shifts
- Ex: Sexual conflict and the arms race in water striders
  - → In striders the optimal mating rate is lower for females than males
    - → Females store sperm, mating has costs for females (Ex. predation)

→ **Bateman's principle** → females almost always invest more energy into producing offspring than males invest

→ Therefore, females tend to resist most mating attempts by males

→ Males have evolved grasping structures to overcome resistance

  → Females evolve behaviours to aid in resisting

→ This antagonistic co-evolution has the potential to escalate like an arms race

  → Evolution of antennal armaments in Rheumatobates (Nature, 2002)

  → Predicts that armaments over time show up as gains on a phylogeny

  → Gains: 17 additional armaments to overcome behavioural resistance

    → Consistent with antagonistic co-evolution

  → Gains of male armaments are much more common, suggesting an arms race over evolutionary time.

LECTURE 22: CONTEMPORARY EVOLUTION AND INVASIVE SPECIES

1. What are biological invasions?
2. Traits commonly associated with invasion success
3. Phenotypic plasticity vs. local adaptation in invaders
4. How can we control invaders?

Biological invasions

- The successful establishment of a species in a region not previously occupied followed by rapid range expansion
- Do not always involve harmful species but most do

Native: Indigenous species that occurs wild in a given region

Alien: A species that has been introduced to a part of the world which it is not native

- Also referred to as adventive, exotic, introduced or invasive species
- Examples of Invasive species:
  → *Lantana camara* invasions in India threaten Tiger habitat
  → Cane toad (*Bufo marinus*) invasion of Tropical Australia
    → Cane toad native to neotropics and introduced to Puerto Rico & Hawaii where it successfully controlled cane beetles devastating sugar cane crops
    → Later introduced to Australia but not successful in reducing beetles and multiplied prolifically reducing biodiversity, especially reptiles
  → Introduction of the Nile Perch to African Lakes has resulted in the extinction of endemic cichlid fish species
  → The battle to prevent 'Asian Carp' invading the Great Lakes

Negative environmental consequences of biological Invasions

- Disrupt ecological processes in natural plant & animal communities
- Displace native species leading to their extinction
- Adverse effects on human health
- Serious economic & social impacts through reduction of yields in agriculture & fisheries

Invasive species in the USA

- Economic cost = $120 billion per year
- 50,000 introduced species, number rising
- ~ 42% of threatened & endangered species at risk primarily due to alien invasives

Questions on invading species

- Why are invading species usually only aggressive in their introduced not their native ranges?
- Are certain ecosystems more susceptible to invasions than others?
- What are the ecological & genetic characteristics of successful invaders?
- Is their evidence for the contemporary evolution of local adaptation in invaders?
- How can invaders be controlled?

Enemy Release Hypothesis:

- Plant species on introduction to an exotic region experiences a decrease in regulation by herbivores and other natural enemies
  → rapid increase in distribution and abundance
- Ex: Differences in enemy attack in populations of white campion (*Silene latifolia*) from Europe and North America (Lorne Wolfe, -- American Naturalist, 2002)
  → Native to Europe, Western Asia, Northern Africa
  → Alien to North America – Now **Naturalised**

→ Specialist and generalist pest and disease pressure was 17 x higher in the native range compared to the alien range

Invasive species thrive in disturbed sites: the more disturbance, the more vulnerable to invasion
- Disturbance can be caused by humans – Amazon forest; or Natural – Volcanic eruption, forest fire

Common attributes of successful invasive species
- Rapid development to reproduction
- High reproductive output
- Well-developed dispersal mechanisms
- Broad ecological tolerance
- High phenotypic plasticity
    - → **Plasticity**: The ability of a genotype to alter its phenotype in response to environmental change – important trait in unpredictable environments

Evolution in invasive species of agriculture
- Selection of barnyard grass plants that mimic cultivated rice (SE Asia, Latin America, Africa)
    - → Weed removal involves ability to distinguish visually between crop and weed
    - → Weeds that look more like the crop escape detection → inadvertently selecting for mimicry
- Selection of herbicide resistant weed species (worldwide)
    - → Widespread adoption of herbicide spraying in mid-to late- seventies' → inadvertently selecting for weed strains resistant to herbicides

Invasive species in Ontario
- Zebra mussels (*Dreissena polymorpha*)
    - → Freshwater mollusk native to Eurasia arrived in ballast water of ocean-going freighters in late 80's
    - → First reported in 1988, now abundant throughout Great Lakes
    - → Single female can produce 30,000 – 1 million eggs per season, free swimming larvae easily dispersed in water
    - → Extensive damage to water intake pipes and commercial & sport fisheries
    - → Filter feeders → have increased water quality
    - → Source of avian botulism leading to death of many birds
- Purple loosestrife (*Lythrum salicaria*)
    - → Aquatic perennial with showy purple flowers native to Europe; used as an ornamental.
    - → Multiple introductions to eastern North America during past century followed by invasion of wetlands
    - → Plants competitive with high phenotypic plasticity, produce millions of small, easily dispersed seeds with high viability
    - → Populations genetically diverse due to multiple introductions, outbreeding and polyploidy; provides opportunities for evolution of local adaptation
    - → Is there evidence for rapid adaptive evolution in invasive populations of Purple Loosestrife? (Rob Colautti, 2009 – Proc Roy Soc B, 2010)
        - → Flowering time correlated with latitudinal gradient of seasonality
        - → Common garden studies indicate significant genetic differentiation among populations
        - → Variation forms a **cline** in time to flowering with northern populations flowering faster than southern populations
            - → Cline: A gradual change in trait means over a geographical transect
        - → Populations farther north have adapted to shorter growing season

Aquatic plant invasion in the tropics -- The world's worst aquatic invaders:
- Water hyacinth (*Eichhornia crassipes*)
    - → Native to lowland South America, now worldwide in tropical & warm temperate regions
- Kariba weed (*Salvinia molesta*)
    - → Genetically sterile floating fern
- Both native to South America, introduced by humans to Old World tropics,
- Free-floating with prolific clonal propagation
- Populations genetically uniform
- Tnvasiveness due to high phenotypic plasticity NOT genetic diversity
- Herbicide control causes pollution of aquatic habitats so biological control methods used

Management of invasives – methods of control
- Mechanical Ex: hand weeding, machines
- Chemical Ex: herbicides, pesticides
- Ecological Ex: burning, flooding
- **Biological control**
    - → The planned introduction of natural enemies (e.g. predators, parasites, pathogens) to control unwanted populations of invaders in alien range
    - → Mode of reproduction of plant invaders & likelihood of success from biological control (Burdon & Marshall, 1981 – J. Appl. Ecology)
        - → Asexual species easier to control than sexual species
            - → Influence of reproductive systems on genetic diversity
            - → Genetic diversity will determine whether resistance evolves
    - → Advantages
        - → Non-toxic to humans; if conducted carefully no serious environmental impacts
        - → If successful the effects are permanent
        - → Economically cheap ($1 for biological control vs. $5 for chemical control)
    - → Dangers
        - → Sloppy science creates new invasion

LECTURE 23: BIODIVERSITY, EXTINCTION AND EVOLUTIONARY BIOLOGY

1. Ecological & evolutionary consequences of global environmental change
2. What is biodiversity and why does it matter?
3. The causes of extinction today
4. Conservation biology – ecological & genetic perspectives on a crisis-driven science

- Amazon – logging of tropical forest for cattle farms

Today's global environmental problems
- Global warming & climate change
- Loss of biodiversity
- Environmental pollution
- Human famine
- Spread of infectious diseases
- Human population growth

Greenhouse gas emissions
- Longest direct measurements of CO2 in the atmosphere
- Atmospheric CO_2 has increased steadily since 1960
- Increase in CO_2 a result of the burning of fossil fuels – Human impact

How will organisms respond to climate change?
- Migrate to more favourable environmental conditions (=ecology)
- Adapt to changing environmental conditions (=evolution)
- Go locally (or globally) extinct (=evolution)

Climate change alters **phenology**, but how much of this response is evolution?
- Phenology – study of periodic plant and animal life cycle events and how they are influenced by seasonal climate variations and habitat factors

Can drought cause rapid contemporary evolution by natural selection? (Art Weis, EEB)
- Directional selection on flowering time in field mustard
- Evidence for directional selection for early flowering as an evolutionary response to drought
  - → Set more seed than later flowering plants

Biodiversity
- "the variety of life on earth"
- The number and kinds of living organisms in a given area
- Two elements:
  - → Interspecific variation or species diversity (studied by ecologist)
  - → Intraspecific variation or genetic diversity (studied by geneticists)
- Four components
  - → Species diversity
  - → Ecological (functional) diversity
  - → Genetic diversity
  - → Phylogenetic diversity
- Loss of biodiversity is irreversible and consequences are least predictable – E.O. Wilson (1989)
- Twenty-five biodiversity hotspots identified around the globe, receiving special conservation efforts

Extinction is natural but its current rate is not!
- Extinction is the permanent elimination of a species – extinction is forever!

- Extinction is a normal evolutionary process; 99% of all species that have ever lived are now extinct
- During the past century massive habitat destruction, particularly in tropical regions, has increased rates of extinction
- Studies of the causes of extinction require demographic and genetic investigations on the causes of rarity
- Three types of extinction
  - → Background extinction
    - → Turnover of species at a low rate, a natural feature of ecosystems
    - → Estimated at ~1 species per year
  - → Mass extinction
    - → Very large numbers of extinctions due to natural catastrophes
  - → Anthropogenic extinction
    - → Caused by humans now estimated at 4-6000 species per year
- Major causes of species extinction today
  - → Habitat destruction
  - → Overexploitation of species
  - → Introduction of pests, predators & competitors

Conservation Biology
- The study of those species, ecological communities & ecosystems being negatively affected by human activities
- Provides the biological concepts & tools for preserving biodiversity & ecosystem function
- Multidisciplinary but with a core ecological and genetic framework
- Ecological issues in conservation biology
  - → Community-level studies
    - → Habitat preservation & the maintenance of species diversity
    - → Application of island biogeographic theory to design of nature reserves
    - → SLOSS: Single large vs. several small
      - → Debate in ecology and conservation biology
      - → What is more effective?
        - → Single large community of organisms?
        - → Several small?
  - → Studies of individual species
    - → Effects of habitat fragmentation on population ecology & demography
      - → Habitat fragmentation of the Atlantic coastal forest of Brazil during the past 60yrs threatens the endemic golden lion tamarin
    - → Keystone species
      - → Beaver – Has ability to create dams and manipulate waterways
    - → Minimum viable population sizes
      - → The number of individuals necessary for a species to maintain or increase its numbers in a region
      - → The smallest population of a species that can sustain itself in the face of environmental variation
      - → No single number for all species; will vary
        - → Ex: cats higher than orchids
- Genetic issues in conservation biology
  - → The maintenance of genetic diversity in rare & endangered species
    - → Relation between heterozygosity & fitness

- → Preventing inbreeding & inbreeding depression
  - → Reducing the stochastic loss of genetic diversity from small populations
- → Genetic consequences of small population size → Mating among relatives
  - → Loss of heterozygosits
  - → Inbreeding depression
    - → Strategies for reducing inbreeding depression in small populations of captive animal species
    - → Founding Individuals:
      - → Speke's Gazelle: 4
      - → Indian Rhino: 17
      - → European Bison: 13
      - → Siberian Tiger: 25
  - → Fixation of deleterious genes
  - → Ex: Cheetah (*Acinonyx jubatus*)
    - → Restricted to two wild populations in southern & eastern Africa
    - → A survey of 52 enzyme loci indicated complete monomorpism.
    - → Other cats have 8-21% of loci polymorphic
    - → High juvenile mortality & low spermatozoal counts
      - → Suggesting inbreeding depression in the species as a whole
    - → It has been proposed that low genetic variation results from an historical bottleneck in population size

Nikolai Vavilov (1887-1943)
- Russian crop geneticist and founder of crop genetic resource conservation

Hunt for wild cotton
- Gene pool collecting expedition to NE Brazil, Jan-May, 1971
- Discovered *Gossypium mustelinum* – wild cotton

Last thoughts
- Future requires fresh ideas and changing paradigms

Reading Summary: Notes and quotes from Coyne - Chapter 7:

25) Gerber L. 2010. Conservation biology. *Nature Education Knowledge* 1(11):14
http://www.nature.com/scitable/knowledge/library/conservation-biology-16089256

Conservation Biology: A multidisciplinary science developed to address the loss of biological diversity
- Evaluates human impacts on biological diversity
- Develops practical approaches to prevent extinction of species

Evil Quartet
- Habitat loss and fragmentation
- Overharvesting
- Introduced predators and competitors
- Indirect effects of these threats on ecological interactions

Conservation Biology aims to provide answers to specific questions
- Point of view of resource managers
- Best strategies for protecting threatened species
  - → Nature reserves
  - → Breeding programs
  - → Reconciling conservation concerns with needs of local people

- Interface between theory and practice
  - → Statistical and computational tools integral in development of analytical methods to address issue of uncertainty

Statistical and computational tools
- Population Viability Analysis
  - → Evaluates full range of forces impinging on populations
  - → Makes determinations about viability
  - → Not viable for predicting when species will go extinct
  - → Useful for comparing relative extinction risks among species and populations and for prioritizing research and management actions
- Minimum Viable Population
  - → Threshold below which populations can no longer sustain themselves
  - → Allows a quantitative "rule of thumb" estimate of minimum population size
  - → Useful for estimating effective population size and timeframe of concern
- Decision Analysis and Multiple-Criteria Approaches
  - → Tool for guiding business decisions under uncertainty
  - → Uses statistical approaches
  - → Additional analysis are necessary to develop and refine analytical tools

Broad Speculation on the Future of Conservation Biology
- A burgeoning discipline since its inception
- Lack of adequate funding remains a critical problem
- Current models have drawbacks
- Precise role of conservation biologists as advocates between conservation priorities and human needs has yet to be formalized
  - → Most scientists are not trained to be advocates
- Many of the theoretical underpinnings of conservation biology are misguided in that they treat an effect, such as small population size, as if it were a cause.
- Conservation efforts should instead be focused on determining causes of population declines and the means by which agents of a decline can be identified
- This idea has reoriented many theoreticians to consider the broader scope of their work and has encouraged field biologists to more closely align their research to conservation-related questions

(26) Kearns C. 2010. Conservation of biodiversity. *Nature Education Knowledge* 1(9):7
http://www.nature.com/scitable/knowledge/library/conservation-of-biodiversity-13235087

Conservation of Biodiversity
- Over 95% of the species that ever existed have gone extinct. Should we be concerned about current extinction rates and conserving biodiversity?
- Modern extinction rates are at 100-1000 times greater than background extinction rates calculated over previous eras
- New species appear, existing species go extinct at a rate 1000 times that of species formation
- The International Union for the Conservation of Nature estimates that 22% of known mammals, 32% of amphibians, 14% of birds, and 32% of gymnosperms (all well-studied groups) are threatened with extinction
- For the first time in Earth's history, a single species, *Homo sapiens*, could cause a mass extinction, precipitating its own demise

Species diversity

- The greatest metabolic diversity is found among the prokaryotic organisms of the Eubacteria and Archaea
- Most new species identified are insects, microbes and fungi, we are still discovering new vertebrates
    - → New species of baleen whale and a clouded leopard. Since 2000, 53 new species of primates have been described including a new species of Brazilian monkey, Mura's saddleback tamarin.

Genetic diversity

- Genes are responsible for the traits exhibited by organisms and, as populations of species decrease in size or go extinct, unique genetic variants are lost.
- Genes hold "genetic potential." For example, many of the crops that we grow for food are grown in monocultures of genetically homogeneous individuals.
    - → Because all individuals are the same, a disease, insect pest, or environmental change that can kill one individual can destroy an entire crop.
    - → Most high-yield varieties show significant reductions in yield within about 5 years, as pests overcome the crops' natural defenses.
    - → Plant breeders look to wild plant relatives to find new genetic varieties and introduce these genes into crops to renew their vigor
        - → 96% of the 7,098 US apple varieties cultivated prior to 1904, 95% of the US cabbage varieties, and 81% of tomato varieties, are extinct, and the genes that made these varieties unique are gone.
    - → The **Red Queen Hypothesis** states that organisms must continually evolve, or succumb to their predators and parasites that *will* continue to evolve
    - → In addition to traditional breeding, advances in genetic engineering have allowed scientists to introduce beneficial genes from one species to another

Ecosystem Diversity

- Ecosystems include all the species and the abiotic factors characteristic of a region.
- When ecosystems are intact, biological processes are preserved
    - → Nutrient and water cycling, harvesting light through photosynthesis, energy flow through the food web, and patterns of plant succession over time
    - → A conservation focus on preserving ecosystems not only saves large numbers of species but also preserves the support systems that maintain life

Biological resources

- Biological resources are those products that we harvest from nature
    - → These resources fall into several categories: food, medicine, fibers, wood products, and more
- For example, over 7,000 species of plants are used for food, although we rely heavily on only 12 major food crops
- Most of the human population depends on plants for medicines
    - → Original formulas for many medicines were derived from plants
- Fibers for clothing, ropes, sacking, webbing, netting, and other materials are provided by a large number of plants
- Trees provide the wood products used in making homes, furniture, and paper products
- Living organisms provide inspiration for engineers seeking better and more efficient products
    - → biomimicry is the study of natural products that provide solutions to human needs
        - → Shark skin provided the model for hydrodynamic swimming suits.

        - → The glue used by Sandcastle worms (*Phragmatopoma californica*) to cement together their sand particle shells was the inspiration for a glue that mends fractured bones in the aqueous internal environment of the body
        - → Scientists are using the chemical nature of spider's silk to design strong, lightweight fibers

Ecosystem Services

- Ecosystem services are processes provided by nature that support human life
- includes the decomposition of waste, pollination, water purification, moderation of floods, and renewal of soil fertility
- Ecosystem processes are often overlooked, and are not generally valued as part of the economy until they cease to function
- When economic value is assigned to these services, it is often startlingly high.
    - → insect pollinators help produce many commercially important fruits such as almonds, melons, blueberries, and apples
    - → The global economic value of pollination services performed by insects has been valued at $217 billion per year
- Rain water is filtered by soil and by microbes that can break down nutrients and contaminants, and reduce metal ions, slowing their spread into the environment
    - → Wetland and riparian plants absorb nitrogen, and trap sediments that decrease water quality.
- Human construction and development disrupt natural environments, but most habitats have an extraordinary ability to recover when given the chance
    - → Dormant seeds in the soil can germinate, stabilize the soil, and initiate successional events that restore vegetation which provides food and structure for other colonizing organisms
- Native plants like fireweed can help revegetate an area after fire

Social and Spiritual Benefits

- Conservation has involved protecting nature for the spiritual gifts it provides and protecting sacred places in the local landscape
    - → indigenous people incorporate detailed knowledge of the animals and plants that make up their world
- The heterogeneity of the world's mythology, folk art, and folk dances show the effects of biodiversity on cultural development, and contribute to the richness of global arts and literature
- Different cultures developed in different landscapes which influenced activities, occupations, diet, language, and architecture
- Biodiversity provides a sense of place
    - → Countries and states have flagship animals and plants that are a source of pride and highlight the uniqueness of each habitat
    - → Ecotourism is travel with the desire to view, sustain, and support natural ecosystems and local cultures
        - → Support from ecotourism can reduce habitat destruction, preserve species that suffer from poaching and illegal trade in the pet market, plus provide jobs for the locals
- in 1892 the US Congress set aside the first national park "for the benefit and enjoyment of the people"
- Frederick Law Olmstead, who in the 1800s designed and managed park systems and urban parks such as Central Park in New York City, believed in the rejuvenating powers of nature

- He felt that contemplating nature's grandeur allowed man to put his life into perspective
- In modern times, with increasing urbanization, people seek out local parks, open space and trails, and travel to national parks and wild places where they can enjoy nature
  - Birding, hiking, fishing, hunting, gardening, and other forms of recreation in nature are popular activities, and are economically important

Glossary: Topics & Concepts

Adaptive radiation: The evolution of ecological and phenotypic diversity within a rapidly multiplying lineage as a result of speciation from a single common ancestor
Allopatric: Speciation that occurs due to geographical separation
Bateman's principle: Females almost always invest more energy into producing offspring than males invest
Clade: Monophylum containing a species and all its descendants
Cladistics: Classifying species based on phylogenetic relationships and shared characteristics
Cline: A gradual change in trait means over a geographical transect
Continuous traits: Complex inheritance by polygenes of small effect with quantitative inheritance and a continuum of outcomes
Convergence: When structures that evolve separately perform similar roles due to similar ecologies
Discrete traits: Inherited by 1 or 2 major genes with homozygous or heterozygous outcomes
Homology: Similarity of traits due to shared ancestry
Homoplasy: Similarity of traits as a result of convergent evolution
Key innovation: Origin in a novel trait resulting in an adaptive radiation which can exploit new resources or habitats previously unavailable prior to trait acquisition
Monophyletic: Arise from a single ancestor single ancestor
Naturalisation: A process by which an alien species spreads into the wild and reproduces sufficiently to maintain its population
Non-monophyletic: Arise from two or more ancestors
Phenetics: Classifying species based on overall resemblance
Phylogentics: Study of evolutionary relationships among species
Plasticity: The ability of a genotype to alter its phenotype in response to environmental change – important trait in unpredictable environments
Polyploidy: Having more than two complete sets of homologous chromosomes
Sympatric: Speciation occurring where a subset of the population becomes genetically different, Ex: through polyploidy
Taxonomy: The theory and practice of classification

geographic variation, population differentiation, gene flow, models of population structure, stochastic processes, genetic drift, genetic markers, measuring gene flow, transgenic escape, tristyly and its inheritance, frequency-dependent mating, equilibrium morph frequencies, evolution of selfing from outcrossing

adaptation, types of selection on quantitative traits, measurement and response to selection, evolution of cyanide resistance, mechanisms of selection, industrial melanism, heavy-metal tolerance, costs to resistance, experimental evolution in E. coli.

native, alien, biological invasion, invasive species, attributes of successful invasives, disturbance, crop mimicry, herbicide resistance, zebra mussels, purple loosestrife, common garden studies, local adaptation, crop mimicry, water hyacinth, Kariba weed, biological control

– global climate change, rapid evolution, resurrection paradigm, components of biodiversity, biodiversity hotspots, types and causes of extinction, habitat fragmentation, SLOSS, keystone species, MVP, inbreeding in zoo animals, conservation of crop genetic resources

