BIS 2B SPRING 2016
Lectures 26-28

SPECIATION AND THE GENERATION OF BIOLOGICAL DIVERSITY

I. DARWINIAN EVOLUTION AND THE ORIGIN OF SPECIES

1. Darwin's explanation:
    a) Natural selection leads to sufficient divergence among "races" so that they eventually become full-fledged species.
    b) **Problems**:
        1) Lack of explicit mechanism causing reproductive isolation.
        2) How does/can reproductive isolation evolve by selection?
    c) Anagenesis *vs*. Cladogenesis
        1) **Anagenesis**: changes due to selection and random forces (*e.g*., founder effects, bottlenecks, *etc*.) that occur within a lineage through time.
        2) **Cladogenesis**: the generation of new clades or lineages through time (*i.e*., lineage splitting).

II. DEFINITIONS OF SPECIES

1. **The Biological Species Concept**: ***A species consists of groups of actually, or potentially, interbreeding natural populations of organisms that are reproductively isolated from other such groups***.
    a) Breeding units:
        1) Populations/Demes/Gene Pools
        2) Populations *vs*. Species
    b) In other words… ***species are breeding units that are evolutionarily independent from other breeding units*.**
    c) In still other words, SPECIES ARE FUNDAMENTAL EVOLUTIONARY UNITS.
        1) Individuals do NOT evolve (their genetic composition – barring mutation – doesn't change).
        2) Populations and species DO evolve.
        3) ***Species represent separate evolutionary units that can no longer exchange genes, hence evolve independently of each other.***
    d) Problems with the Biological Species Concept
        1) Actual *vs.* potential mating opportunities in **allopatric** (geographically separated) populations.
        2) What's "natural"?
            • Mating in the lab *vs*. in nature.
        3) What about extinct organisms?
        4) What about asexual organisms?

III. TYPES OF GENETIC BARRIERS OR REPRODUCTIVE ISOLATING MECHANISMS

"The evolution of a new species is equivalent to the evolution of genetic barriers to gene flow between populations." (Doug Futuyma)

⇒ WHAT MECHANISMS LIMIT GENETIC EXCHANGE (GENE FLOW) BETWEEN POPULATIONS?
⇒ HOW CAN THESE GENETIC BARRIERS EVOLVE?

1. **Prezygotic Mechanisms**: *Prevent gametes from uniting to form zygotes*.
    - a) Spatial/Geographical Isolation: immediately limits gene flow if there is little dispersal across a geographic barrier
        - 1) The importance of **allopatry**.
        - 2) Example: speciation in snapping shrimp across the Isthmus of Panama
    - b) Ecological Isolation: if two species utilize different habitats (& mate in those habitats), they can be ecologically isolated
        - 1) Example: benthic and limnetic forms of 3-spine sticklebacks
    - c) Temporal Isolation: species that breed at different times (daily, seasonally, or yearly) have limited opportunity to mate
        - 1) Example: periodic cicadas that breed in different prime-numbered years
    - d) Behavioral Isolation: species-specific mate recognition systems (courtship behaviors, songs/acoustical signals, chemical signals/pheromones, visual signals) may effectively limit mating between species
        - 1) Example: species-specific flashing and flight patterns in fireflies
    - e) Mechanical Isolation: anatomical mismatches between males and females may make the physical act of copulation impossible (or close enough)
        - 1) Example: mismatched genitalia in robber flies
    - f) Gametic Incompatibility: even if mating succeeds, gamete recognition systems prevent fertilization between gametes from different species
        - 1) Example: Gamete recognition in purple *vs*. red sea urchins
2. **Postzygotic Mechanisms**: *Act after fertilization has occurred*
    - a) Hybrid Inviability: zygotes are formed, but die before developing into adults
        - 1) Example: *Rana sylvatica* x *Rana pipiens*
    - b) Hybrid Sterility: hybrid zygotes develop into adults, but the adults are sterile (genes "flow" into hybrids but remain trapped there)
        - 1) Example: Zebra (male) x Horse (mare) ⇒ Zorse (Sterile)
    - c) Hybrid Breakdown: fertile hybrids are formed but they have very low mating success (or backcrosses produce offspring with low fitness)
        - 1) Example: Mallard x China Duck ⇒ Challard (or Muck)

IV. THE EVOLUTION OF REPRODUCTIVE ISOLATION

1. ***How can a trait that almost by definition reduces the fitness of its bearer increase in frequency?***
    - a) In other words, how can a mutant that prevents an individual from mating with other members of its population spread in the face of other alleles that do not reduce mating opportunities?
2. **The Problem**: ***Gene flow (even a little bit) prevents population differentiation***.
    - a) On average, ***the exchange of one (1) migrant per generation between populations is sufficient to prevent those populations from diverging***.
    - b) There must be some EXTRINSIC barriers that initially limit gene flow.
3. The importance of phylogenies:
    - a) A phylogeny is a graphical depiction of the history of relationships among a group of organisms.
    - b) Key terms & concepts:
        - 1) **Sister species**: a pair of species that share a single most recent common ancestor – they are each other's closest relatives

2) **Node**: a branching point on a phylogeny – nodes are the result of a speciation event in the past
3) **Monophyletic clade**: a taxonomic group that includes ALL of the taxa/species descended from a specific common ancestor.
4) **Paraphyletic clade**: a taxonomic group that excludes some of the descendants from a specific common ancestor.
5) **Polyphyletic clade**: a taxonomic group that does not contain the most recent common ancestor of its members.

4. Three geographic scenarios that could reduce/eliminate gene flow (geographic classification):
    a) **Geographic Isolation/Allopatric Scenarios**: Populations have discrete ranges ⇒ *geographical barriers limit gene flow*.
        1) *Vicariant Models*: some kind of geographic barrier arises that subdivides a formerly interconnected set of populations
            - Diversifying or other forms of selection could then promote differentiation between populations living in different habitats.
            - Example: Speciation in snapping shrimp across the Isthmus of Panama
        2) *Dispersal Models*: a few “lucky” dispersing propagules cross a geographic barrier, and successfully colonize a new habitat.
            - **Founder effects** and **genetic drift** in **small** populations promote population differentiation
            - Example: Speciation and **adaptive radiation** in Hawaiian *Drosophila*
        3) **Secondary contact**: *What happens when a geographic barrier disappears and two geographically isolated populations come back into contact?*
            - Complete isolation and no hybridization ⇒
            - Hybridization, introgression, and the merging of populations.
            - Partial isolation and **reinforcement**: selection acts to reduce matings between the parental populations when they produce hybrids with low relative fitness
    b) **Parapatric Scenarios**: Populations have abutting ranges ⇒ Environmental discontinuities can limit gene flow.
        1) Example: Speciation on mine tailings in pasture grass (*Agrostis tenuis*)
            - Secondary evolution of divergent flowering times (late *vs*. early flowering)
    c) **Sympatric Scenarios**: Populations/incipient species have overlapping ranges
        1) Primary sympatry *vs*. secondary sympatry
            - Primary sympatry: Species differentiated in sympatry (*true sympatric speciation*).
            - Secondary sympatry: Species differentiated in allopatry or parapatry.
                ⇒ After becoming reproductively isolated, the populations moved into sympatry (not the condition under which reproductive isolation evolved).
            - Using phylogenies for distinguishing between primary *vs*. secondary sympatry
        2) Mechanisms of sympatric speciation.
            - *Multiple niche polymorphism*: Sympatric speciation in crater lake cichilds

STUDY QUESTIONS

1. What is the biological species concept, and what are its main criteria for defining a species?

2. Explain why application of the biological species concept is difficult or impossible in each of the following situations: (a) examples of natural hybridization, (b) the existence of strictly asexual organisms, and (c) disjunct (allopatric) distributions of species.

3. Two closely related grasshopper species occur sympatrically. No hybrids have been reported in nature. However, when an evolutionary biologist brings the two species into the lab, she discovers that they can hybridize to produce fertile offspring. How can you explain these observations? Should the grasshoppers be considered separate species?

4. How does natural selection *versus* genetic drift act to promote the evolution of **intrinsic** barriers to gene exchange in allopatric (both vicariance and peripatric/dispersal modes) *versus* parapatric *versus* sympatric models of speciation?

5. Why have island archipelagoes played such an important role in the development of the science of speciation? What lessons have we learned from studies of speciation in places like the Hawaiian Islands?

6. Why do most evolutionary biologists agree that allopatric speciation is common but sympatric speciation is not? Focus your discussion on the fundamental difference between these two alternatives, and why that difference is likely to be important for divergence and the evolution of reproductive isolation.

7. Sympatric speciation is generally thought to be a rare event because sympatry should promote gene flow. Explain clearly the evidence that speciation occurred sympatrically in the crater lake cichilid fish inhabiting Barombi Mbo in Cameroon. In particular, explain how the **phylogenetic relationships** of the 11 species of cichlids in this lake support the argument for sympatric speciation. How does this contrast with the phylogenetic evidence for vicariant allopatric speciation in snapping shrimp? Be sure that you can look at a phylogenetic tree and understand whether its structure is consistent with sympatric *versus* allopatric scenarios for the evolution of reproductive isolation.

8. Compare and contrast, using a phylogeny from lecture or the book, the differences between monophyletic, paraphyletic, and polyphyletic clades/taxa. Why are Reptilia without birds (Aves) paraphyletic? Why do evolutionary biologists aim to name only monophyletic taxa? Why are non-monophyletic taxa a problem? Do **sister species** represent a monophyletic taxon?

9. An island in an isolated oceanic archipelago of recently formed (the last few million years) volcanic islands is colonized by three mainland species of beetle. The three species differ in several important characteristics (see table on the next page). What do you predict will be the patterns of diversification and speciation for the three descendant lineages? Explain how the differences in dispersal potential, feeding ecology, population size, and mating behaviors affect the potential for speciation in each of the three species.

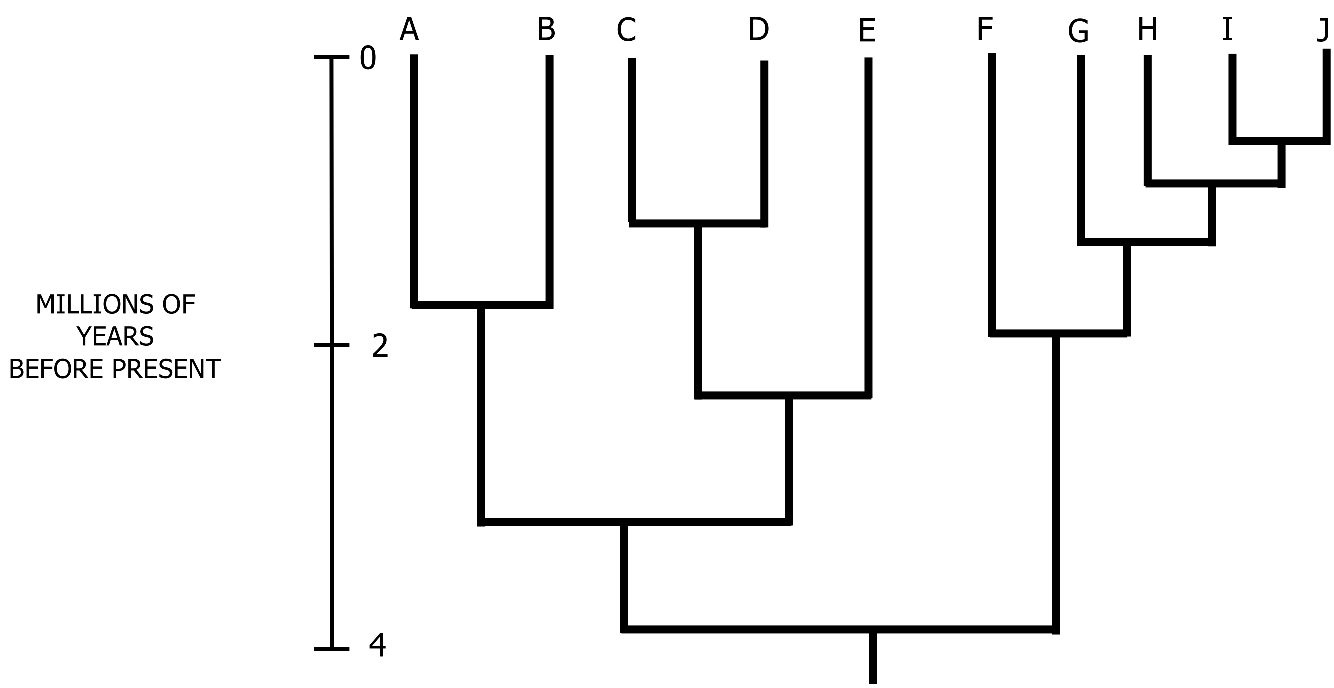
	SPECIES 1	**SPECIES 2**	**SPECIES 3**
FLIGHT	Strong flier over long distances	Flightless*	Flightless
POPULATION SIZE & STRUCTURE	Large, continuous	Small, patchy	Small, patchy
HOST PLANTS	Feeds on many different plants	Very host specific feeding, but do NOT mate on host plant	Populations tend to feed AND mate on one or a few plant species. There is intraspecific variation for host preferences.

10. With respect to the phylogeny shown below, which of the following statements is ***TRUE***:

a) Species F, G, H, I, and J form a **polyphyletic** group.
b) Species A, B, C, D, and E form a **paraphyletic** group.
c) Species A, B, I and J form a **monophyletic** group.
d) Species F, G, and H form a **monophyletic** group derived from the same common ancestor.
e) Species C, D, and E form a **monophyletic** group.

11. In the phylogeny shown below, what is the ***fewest*** number of speciation events that could have given rise to the clade that includes species A, B, C, D, and E?

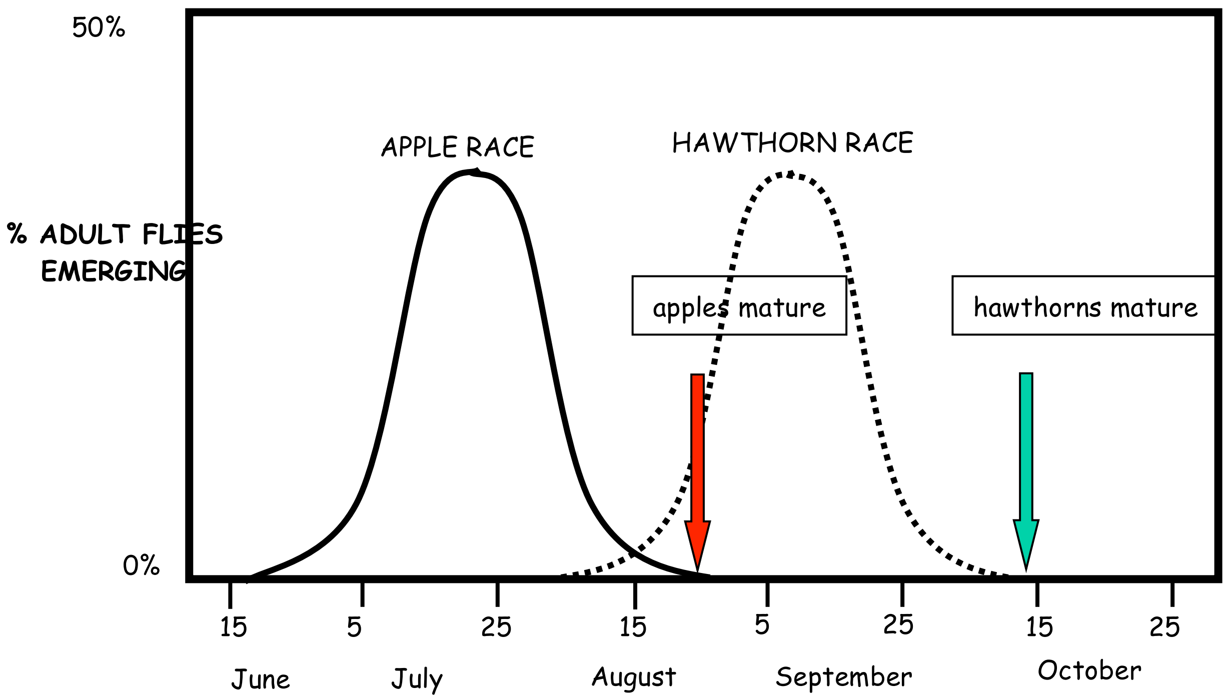
a) 4
b) 6
c) 8
d) 3
e) 11



12. In apple maggot flies, *Rhagoletis pomonella*, adults and larvae feed on very specific host plants. There are at least three genetically distinct lineages, one of which specializes on hawthorn trees, another specializes on apples, and the third specializes on cherries. They are pretty good fliers, easily capable of moving several kilometers a day. They can also mate with each other, and the hybrids are fertile.

In the example shown below, there are only apple or hawthorn trees available for the maggot flies. Assume that apple specialists feed and mate primarily on apples, and that hawthorn specialists feed and mate primarily on hawthorn fruits. (Sometimes, though, **if it were available**, an apple specialist might feed on a hawthorn, and a hawthorn specialist might feed on an apple.) Adult flies emerge a few weeks before their preferred fruit matures, fly around for awhile, then lay eggs on their preferred host (where their larvae feed and develop).

What are the main barriers to gene flow between these two races? What, if any, is the importance of timing of fruit maturation in this scenario? How would you expect changes in timing of fruit maturation to affect the likelihood that hybrids would be formed? Assume that the apple and hawthorn races were good biological species? How could you distinguish whether they speciated sympatrically or allopatrically?



13. Why do most evolutionary biologists agree that allopatric speciation is common, but sympatric speciation is rarer?

a) Because reproductive isolation CANNOT evolve in sympatry.
b) Because sympatric species cannot occupy separate niches.
c) Because there is no extrinsic barrier to gene flow in sympatry.
d) Because inbreeding is too common in sympatry and populations go extinct.
e) Because disruptive selection can only act on allopatric populations.

14. The main problem with understanding how genes responsible for reproductive isolation could increase in frequency is…

a) such genes would reduce the fitness of an individual that carries them.
b) such genes would rapidly spread due to sexual selection.
c) genetic drift would immediately eliminate them from a population.
d) hybrids carrying these genes would be competitively superior to parental genotypes.
e) none of the above.

15. You carefully study adjacent populations of two very similar meadow mice, one from Woodland (about 15 km north of Davis), the other from Davis. You want to know whether the Woodland and Davis populations belong to the same biological species or to two different species. You could ***most confidently*** decide this if you could…

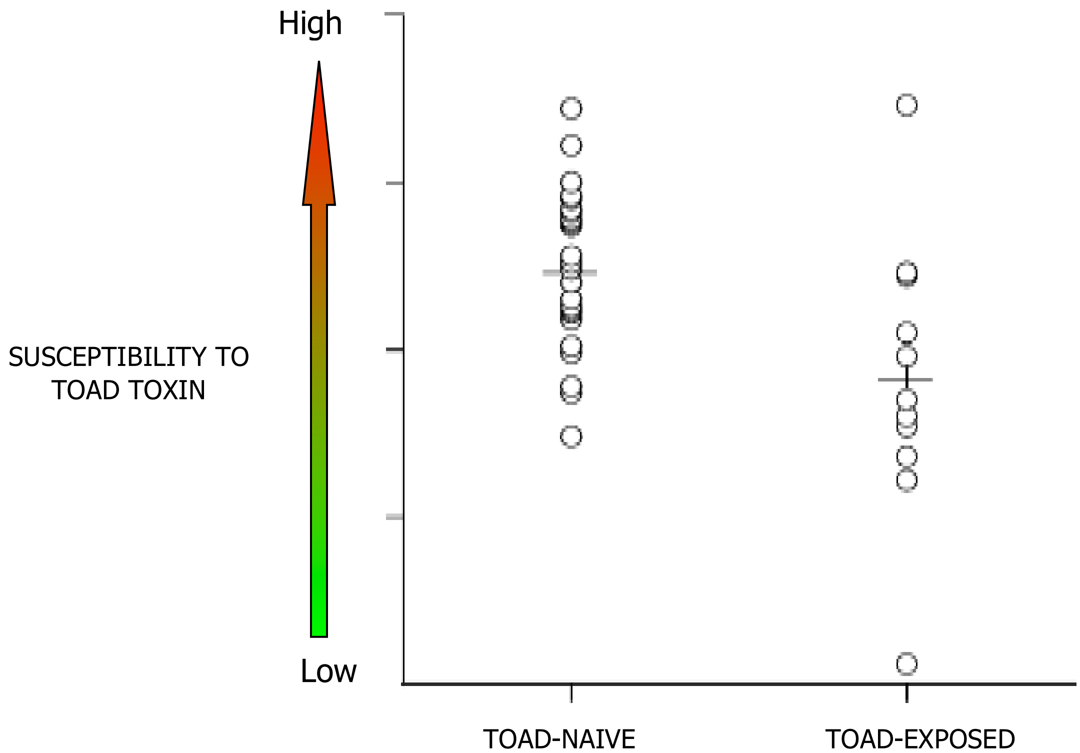
a) show that where the ranges of the two mice overlap there is no hybridization.
b) bring the two types of mice into the laboratory to see if they will mate.
c) demonstrate that the natural ranges of the two types of mice are entirely allopatric.
d) show that there are statistically significant coat color differences between the two types.
e) show that the Woodland mice prefer to eat meat, but the Davis mice prefer to eat tofu.

16. Two species of wild lettuce grow sympatrically, but one flowers in the early spring, and the other flowers in the summer. This is an example of...

a) post-zygotic reproductive isolation
b) gametic incompatibility
c) behavioral isolation
d) temporal isolation
e) reinforcement
f) hybrid incompatibility

17. In Australia, when red-bellied black snakes first encountered cane toads, most of the snakes were highly susceptible to the cane toad toxin, and died soon after eating them. The graph shown below compares susceptibility to toad toxin of individual snakes, from two populations, one never exposed to cane toads (TOAD NAÏVE), the other having been exposed to cane toads for 50 years (TOAD EXPOSED). Each point on the graph represents data for a single snake.

You suspect that natural selection has caused the changes shown in the graph. We know that snakes reproduce, meeting the first condition for evolution by natural selection to occur. **What are the additional 3 key conditions that must be met in the snake population in order for natural selection to have occurred? Based on the information in this graph, is there evidence that each of these conditions is met? If so, how is each met? If not, what kind of evidence would convince you?**



Condition 1:

Is condition #1 demonstrated by data in the graph? If yes, how? If not, then what data would convince you?

____

Condition 2:

Is condition #2 demonstrated by data in the graph? If yes, how? If not, then what data would convince you?

____

Condition 3:

Is condition #3 demonstrated by data in the graph? If yes, how? If not, then what data would convince you?

____