Speciation and extinction

But what’s a species; and when you’re dead, you’re dead — unless you’re Homer Simpson...

http://www.snotr.com/video/128
Macroevolution

* Continuum — micro . . . macro . . . .
* Regardless, large, complex changes, e.g. . . .
* Appearance and disappearance of species is generally known as macroevolution.
* Species are distinct organisms, but the definition has changed over time.
So what is a “species?”

- Carolus Linnaeus (1707–1778):
  - “all examples of creatures that were alike in minute detail of body structure”
  - First to give two-word biological names, e.g. Homo sapiens.
  - Hierarchical system of classification.
  - He also came up with higher, more inclusive categories: orders, classes, and kingdoms (some of which are still used today).
  - However, not based on evolutionary relationships.
  - Linnaeus thought that all critters were independent, unchangeable, ‘special creations.’
Along came Darwin . . .

- Darwin connected species diversity to evolution and was the first to consider classifications as genealogies, “our classifications will come to be as far as they can be made, genealogies.”

- Classification schemes came to be thought of as hypotheses about the evolution of all of life! Good.
The biological species concept:

- **Ernst Mayr (late 1940’s):** A species is...
  - A population, or group of populations, whose members can interbreed and produce fertile offspring.
  - Speciation occurs when members of a population can no longer interbreed.
  - Microevolution becomes macroevolution.
  - However the potential to interbreed does have problems with asexual organisms, hybridization, and extinct organisms.
DNA sequence analysis has refined the definition considerably!

* But even this is tough. How similar should the DNA be, to be considered the same species? Which genes should be used, or perhaps the entire genome?
* And what about horizontal transfer?
* See the “Bar-Code of Life” project: http://www.barcodinglife.org/
An example in lemurs...

Prior to 1993 there were only considered to be two species of mouse lemurs.

Now we know that there are at least sixteen, more likely nineteen, different species based on DNA sequence analysis.

A. Yoder's group, Duke University
These guys are an example of a “cryptic species.”

They look pretty darn similar to us, but they’re nocturnal!

Turns out they use different ‘chirp’ calls!
Mayr’s revision (1995)

“The actual demarcation of species taxa uses morphological, geographical, ecological, behavioral, and molecular information to infer the rank of isolated populations.”

Takes into account all data available!
How’s it happen — Reproductive barriers

* Prezygotic barriers prevent fertilization:
  * Ecological or habitat isolation – physical separation;
  * Temporal isolation – differences in timing;
  * Behavioral isolation – e.g. intricate mating dances;
  * Mechanical isolation – reproductive anatomy;
  * Gametic isolation – important in external fertilization.

* Postzygotic barriers prevent viable or fertile offspring:
  * Hybrid inviability – embryo dies early;
  * Hybrid infertility – mules are infertile.
Some examples of prezygotic reproductive isolation are shown here.

**Ecological (habitat) isolation**
Different environments (e.g. desert fox and arctic fox)

**Temporal isolation**
Active or fertile at different times (e.g. two species of field crickets reproduce in different seasons)

**Behavioral isolation**
Different activities (e.g. different flash patterns in firefly species)

**Gametic isolation**
Gametes cannot unite (e.g. mouse and rat)
And postzygotic . . .

Postzygotic Reproductive Isolation

**Hybrid inviability**
Gametes unite, but development cannot produce a viable embryo (e.g. goat and sheep)

**Hybrid infertility**
Hybrids lack the ability to make or deliver viable gametes (e.g. liger, the hybrid offspring of a lion and a tiger)

(top left): © S.E.Arndt/Peter Arnold, Inc.; (top right): © David Dalton/Bruce Coleman, Inc.; (bottom): © GERARD LACZ/Animals Animals - Earth Scenes
Three main modes of speciation:

- **Allopatric speciation** – a geologic event or structure physically separates a population into two or more groups.

- **Parapatric speciation** – part of a population enters a new habitat bordering on the range of the parent species.

- **Sympatric speciation** – populations diverge genetically while living in the same physical area.
Let's look at examples of each . . .

- **Allopatric speciation**
  - No contact between populations

- **Parapatric speciation**
  - Populations share a border area

- **Sympatric speciation**
  - Continuous contact between populations

* a schematic overview, then in detail
Allopatric speciation

Physical separation, e.g., Tamarins in the Amazon, and Pupfish in Death Valley.
Parapatric speciation

Speciation on the border . . .

Border group possesses a diverging and unique combination of traits, e.g. Little Greenbul of Cameroon

More robust in the ecotone.

Frailer in the rain forest.
Sympatric speciation

Cichlids in Africa – microenvironments, but this is really just a gradient – where does allopatric stop and sympatric begin?

Two different Clarkias in California – following a severe drought bottleneck event.
Also, sympatry due to polyploidy... 

Numbers of sets of chromosomes increases, e.g. Cotton. Quite common in plants. Very rare in animals.
Pace of evolution

* Gradualism:
  * Evolution proceeds in small, incremental changes over many generations;
  * Most of the time fossils are not created, so transitional form evidence is often missing.

* "Punctuated equilibria: an alternative to phyletic gradualism" (Eldredge and Gould, 1972, in Models in Paleobiology):
  * Long periods of stasis alternating with relatively brief (tens of thousands of years) bursts of fast evolutionary change.
  * The fossil record reveals that both occur!
Schematically...
Punctuated Equilibrium and hopeful monsters?

* It’s easy to imagine how the raw material for microevolution can feed gradualism;
* But where the heck do some of the larger changes associated with punctuated equilibrium come from (besides just lots of microevolution over many generations)?
* Two major sources —
  * Regulatory systems, e.g. the HOX genes;
  * Gene and genome duplication, e.g. fishes.
Regulatory effects

“Comparisons of developmental gene regulation between morphologically divergent animals, analyses of intraspecific variation, and the response of organisms and genes to selection all support the claim that regulatory DNA is the predominant source of the genetic diversity that underlies morphological variation and evolution.”

Sean Carroll (2000)
Regulation of *Hox* gene expression in the vertebrate hindbrain

These genes regulate the ordering of body parts along the length of animal bodies.

**e.g. HOX**

Carroll et al. (2001) “From DNA to Diversity”
Gene and genome duplication

Evolution by Gene Duplication

“Had evolution been entirely dependent upon natural selection, from a bacterium only numerous forms of bacteria would have emerged. The creation of metazoans, vertebrates and finally mammals from unicellular organisms would have been quite impossible, for such big leaps in evolution required the creation of new gene loci with previously non-existent functions.” (Susumu Ohno, 1970)
E.g., a fish-specific genome duplication precedes the diversification of ray-finned fishes.
These two methods can combine.

One mechanism of divergence in gene function - combining gene duplication and regulatory evolution
Adaptive radiation; the usual examples:

- Population faced with a diverse environment gives rise to multiple specialized forms in a relatively short time because of strong selection and genetic drift compounded by the Founder effect. Therefore, . . .
- Speciation can happen in ‘rapid’ bursts.
- Especially, with individuals colonizing new, isolated habitat, e.g. . . .
- Galapagos Island finches and tortoises,
- African lake cichlids, Madagascar lemurs,
- And anoles in the Greater Antilles.
Cichlids in Africa

Diversity and evolution of cichlid fishes

Out of Lake Tanganyika: Origins of the Lake Victoria and Malawi species flocks

~ 1,800 species
(>7% of all teleosts)

haplochromines

Lake Victoria superflock:
~ 100,000 years old
Verheyen et al. (2003) Science

“Out of Tanganyika”

Another cichlid example

The Midas cichlid species complex in Nicaragua

*Amphilophus from Nicaragua*: A highly polymorphic cichlid species complex

Anole lizards in the Antilles:

Other examples occur where some members of a population inherit a selective advantage; e.g., bird flight, photosynthesis.
Another example of adaptive radiation can occur after a bottleneck...

Survivors get through some major environmental change; e.g. mammals after the fall of dinosaurs, caused by a huge asteroid impact into the Yucatan.
This was a BIG deal! ~65 MYA

At precisely 65 mya, an asteroid nearly 10 km (6 mi) wide slammed into what is now Mexico's Yucatan Peninsula.
Dust from the impact blocked sunlight from reaching the surface of the entire Earth, making it too dark for photosynthesis for several months up to a few years.
Which leads us to: Extinction . . .

* Which is caused by a failure to adapt to environmental change.
* This could include habitat loss, new predators, new diseases, . . .
* Sometimes just bad luck.
* A species’ chance of extinction depends on how fast the environment changes relative to the rate the population evolves.
There are two general types of extinction:

* Background extinction rates – a gradual loss of species as populations shrink in the face of new challenges:
  * 0.1 to 1.0 species per year per million species, over the history of the earth.

* Mass extinctions – a great number of species disappear over a relatively short time.
  * This periodically opens up vast new habitats for adaptive radiation.
This is seen in the history of life on the earth — here marine critters.

The 'Big Five' extinction events!

- End of the Ordovician
- Late Devonian
- End of the Permian - the biggest
- End of the Triassic
- End of the Cretaceous & the dinosaurs
That’s enough on speciation and extinction . . .

* But now we need to pick up on “tree-thinking” . . .
* That is . . .
* Understanding how all of life can be connected on a ‘tree.’
* And how that opens up all sorts of new ways of understanding the world about us.