Overview of Lecture: Speciation & Species Concepts.

Read: Text ch 24

We’ll consider the roles of gene flow and reproductive isolation in local adaptation and speciation & wrestle with various attempts to clearly and usefully define discrete “species.”

Bullet Points:
- biodiversity: within and between species
- gene flow, divergence and local adaptation
- pre & post zygotic isolation
- mechanisms of speciation
- allopatric (apart) & sympatric (together)
- species in a ring
- what is a species?
- definitions: ‘biological’ & phylogenetic
- why it matters
- endangered species act

Links:
- Press release
- More information on the 2007 Red List
The Concluding Passage from *The Origin of Species* by Charles Darwin

... endless forms most beautiful and most wonderful have been, and are being, evolved.

Although Darwin titled his book *On the Origin of Species*, he never clearly defined ‘species,’ nor satisfactorily explained the process of speciation “- that mystery of mysteries - the first appearance of new beings on this Earth.”

He focused on natural selection & adaptation within & between species. {microevol within species rather than the macroevol of diff species}

Genetic & phenotypic divergence & local adaptation require reduced gene flow. Prezygotic & postzygotic barriers isolate the gene pools of biological species.

Genetic (reproductive) isolation & divergence are cause & consequence of speciation.
Although modern evolutionary biology started with a seminal volume whose title identified the origin of species as the central theme (Darwin 1859), the topic of speciation received relatively little attention ...

Darwin and his contemporaries devoted much more attention to explain how changes occurred within species {adaptation} rather than how species originated. {reproductive isolation}

... a search of the published scientific literature using web of science reveals ...

Fig. 1 Number of publications listed in Thomson-ISI web of science with the word speciation in the title since 1901 after that papers referring to chemical speciation have been removed
Mayr (1942) was the first to focus on the importance of species, introducing the biological species concept (BSC), which has dominated speciation research for the past seven decades, and championed the idea of speciation in allopatry. Physically isolated in space

Dobzhansky’s work (1937) pointed out the importance of understanding how changes in allele frequencies could produce genetically distinct groups and the importance of reproductive isolating mechanisms.

Starting in the 1980s, the availability of new empirical tools such as molecular genetics, and theoretical and methodological approaches, such as phylogenetic and comparative methods, led to resurgence in interest in the origin of species.

This resurgence of interest in speciation has been one of the main developments in evolutionary biology during the past 25 years …

… many of the major conclusions about speciation … have been re-examined.

The debate over species concepts … was reinvigorated …

Both empirical and theoretical advances led to questioning the biogeography-centered view of speciation, and the fact that allopatry was the dominant mode of speciation …

… we wish to outline some … questions still worth answering …

Are Species Real?

Do We Need a Universally Accepted Species Concept to Study Speciation?
Gene flow can disrupt local adaptation, resulting in a kind of ‘average’ adaptation that is not ‘perfectly’ specialized to any of the local environments.

Local specialization and maladaptation in the Mediterranean blue tit (Parus caeruleus).

France: repro timed to match food in dominant deciduous
France: repro too early to match food in rare evergreen
Corsica: repro timed to match food in dominant evergreen
Corsica: repro too late to match food in rare deciduous

(1) on a regional scale, each population is specialized to the more common habitat,
(2) in the less common habitats birds are clearly mistimed

{adaptive divergence requires interrupted gene flow: reproductive isolation}
**Figure 24.6 Exploring Reproductive Barriers**

Prezygotic barriers impede mating or hinder fertilization if mating does occur.

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Habitat isolation

- Individuals of different species

Temporal isolation

- Reduced Hybrid Viability
- Reduced Hybrid Fertility
- Hybrid Breakdown

Behavioral isolation

- Reduced Hybrid Viability
- Reduced Hybrid Fertility
- Hybrid Breakdown

Mechanical isolation

- Reduced Hybrid Viability
- Reduced Hybrid Fertility
- Hybrid Breakdown

Gametic isolation

- Reduced Hybrid Viability
- Reduced Hybrid Fertility
- Hybrid Breakdown

- Gametic isolation prevents the crossing of species barriers.

- Sperm and eggs of different species do not fuse.

- The genes of different parent species may interact and impair the hybrid development.

- Even if hybrids are vigorous, they may be sterile. In some cases, the hybrid may fail to produce normal gametes.

- The hybrid offspring may not survive or reproduce.

- Some first-generation hybrids are viable and fertile, but when they mate with one another or with either parent species, offspring of the next generation are infertile or sterile.

- The hybrid offspring of a donkey (e) and a horse (f) is a mule (g), is robust but sterile.

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For the past 50 years or so, many influential evolutionary biologists, have held that physical separation among members of a species, such as that caused by the emergence of a mountain chain, typically drives the splitting of one species into two. Populations separated by geographic barriers can't interbreed and eventually evolve into distinct species. Examples of this speciation process, called allopatry, abound.

Charles Darwin recognized allopatry as a driving force of speciation. But he also thought populations could diverge into separate species in the absence of physical barriers, an idea now called sympatric speciation. However, his successors were at a loss to explain how this could happen, and they could find few examples. By 1907, textbooks dismissed sympatric speciation, and few researchers have taken sympathy seriously. Now the situation is changing fast. ...
We have focused our study on a particular pair of forms within the lake that currently appears to be in the process of speciation. This pair is characterized by an unique breeding colouration and specific morphological aspects … {including size}

It has differentiated into a large inshore and a small pelagic form, apparently as a response to differential utilization of food resources. {body size differences adapted to habitat-food-ecological niche: large inshore eats big insects, snails etc. & small open water eats small plankton}

Still, breeding and brood care occurs in overlapping areas, both in time and space. {sympatric breeding (same place = shallow bottom) gives opportunity to hybridize}

Analysis of nuclear gene flow on the basis of microsatellite polymorphisms shows a highly restricted gene flow between the forms, suggesting reproductive isolation between them.

This reproductive isolation is apparently achieved by size assortative mating, although occasional mixed pairs can be observed.

Our findings are congruent with recent theoretical models for sympatric speciation, which show that differential ecological adaptations in combination with assortative mating could easily lead to speciation in sympathy. {see text pg 497}
What is a species?  

Species is a Latin word meaning “kind” or “appearance.” But are organisms truly divided into the discrete units we call species, or is this classification an arbitrary attempt to impose order on the natural world? To answer this question, biologists have compared not only the morphology (body form) of different groups but differences in physiology, biochemistry, and DNA. The results generally confirm that morphologically distinct species are discrete groups, with many differences in addition to morphological ones.

The Folk Concept of Species  

{Folk} have found that the plants and animals they see can be mentally grouped into a number of taxa, in which the individuals are basically alike {~morphospecies}. Folk taxonomies have two features in common. One is the idea of reproductive continuity within a species. Dogs beget dogs, they never beget cats! The second is that there is a discontinuity of variation between species. In other words, you can tell species apart by looking at them (Cronquist 1988).

The biological species concept defines a species as a population whose members have the potential to interbreed in nature and produce viable, fertile offspring, but are unable to produce viable, fertile offspring with members of other populations. In other words, the members of a biological species are united by being reproductively compatible, at least potentially.
Identifying units for conservation using molecular systematics: the cautionary tale of the Karner blue butterfly.
- mitochondrial DNA indicates some interbreeding w/ Melissa blue
Ring species, which consist of two reproductively isolated forms connected by a chain of intergrading populations, have often been described as examples of speciation despite gene flow ...

Two forms of greenish warbler, one in west Siberia (TL = P. t. viridanus) and one in east Siberia (ST = P. t. plumbeitarsus), **coexist without interbreeding** in central Siberia and can therefore be considered **separate species**.

... amplified fragment length polymorphism (AFLP) markers show distinct differences between two reproductively isolated forms but gradual change around the ring ...

\[ P_{tv} = TL \text{ and } P_{tp} = ST \text{ don’t recognize each other’s songs and won’t mate} \]

**Fig. 1.** (A) Map of Asia showing the range of greenish warblers in the breeding season. Different colors represent different subspecies ...

![Image](image1.png)

The hatched area in central Siberia indicates the overlap zone between *viridanus* and *plumbeitarsus*. The gap in the ring in northern China is likely due to recent habitat destruction.

**Fig. 2.** Genetic distance based on AFLP markers increases with geographic distance around the southern ring.
Darwin wrote about the difficulties associated with species definitions:
‘Nor shall I here discuss the various definitions … of the term species. No one definition has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species.’

The discovery that species evolve and give rise to new species (speciation) radicalized the ages-old conundrum. {discrete categorization of a continuous world}

Biologists of Darwin’s time were familiar with taxonomic puzzles over whether one was dealing with varieties or species.

But with the realization that varieties gradually become species, it seemed for many that … species designations … were in fact truly arbitrary.

Darwin anticipated this (1859, pg 485):
“… we shall have to treat species in the same manner as … genera, … genera are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be free from the vain search for the undiscovered and undiscernable essence of the term species.”

The modern version of this debate lies between various versions of the phylogenetic species concept (~ESU or DPS concepts) and Mayr’s biological species concept.
The biological species concept {~ ‘Could they interbreed?’} has a number of problems that have led scientists to propose alternative species concepts. Some scientists have turned to examining the recent evolutionary history of populations. {not ‘Do they have the potential to interbreed in the future?’, but ‘Have they been interbreeding in the recent past?’, or are the lineages ‘distinct population segments’ DPSs or, equivalently ‘evolutionarily significant units’ ESUs?}

These phylogenetic species concepts are currently a topic of great debate.

For the purposes of this Act- …

(15) The term "species" includes any subspecies of fish or wildlife or plants, and any distinct population segment {DPS} of any species of vertebrate fish or wildlife which interbreeds when mature. {a DPS is considered to be an evolutionarily significant unit (ESU)}
Pacific salmon have been extirpated from nearly 40% of their historical habitat and of the remaining salmon populations, almost one half are thought to be at risk of extinction.

... the potential remedies for the salmon problem have huge implications for the ways people extract water, develop industrial, commercial and private properties, generate electricity, transport goods, harvest fish, ...

Given their propensity to home to natal streams, salmon are naturally subdivided into a hierarchy of genetically distinct groups that tend to show local adaptation ...

... multiple lineages marked by varying levels of evolutionary divergence.

Advances in molecular genetic and statistical tools have led to impressive algorithms for discriminating among groups within species.

... resolution of distinct genetic lineages within a species does not help to identify which hierarchical level of organization is the appropriate one to save.

The NMFS defines reproductively isolated groups of salmon with unique evolutionary legacies as Evolutionarily Significant Units (ESUs).

The NMFS has identified 51 ESUs within the 6 species of Pacific salmonids; for legal purposes they are treated as separate species that must be recovered; 26 of these currently are listed under the ESA
The barred owl, a close relative of the spotted owl, has invaded the Pacific Northwest. This owl can out hunt the spotted owl and is generally more resilient. Worse than that, the barred owls can breed with the spotted owls. Together they create a hybrid owl that can reproduce.

Protection for this species under the Endangered Species Act — where it is listed, when it was listed, and other information.

Similar species:

The Spotted Owl is similar to the Barred Owl but has cross-shaped markings on the underparts where the Barred Owl is alternately barred on the breast and streaked on the belly. Barred Owls are grayer than Spotted Owls. Great Gray Owl is much larger with yellow eyes. Great Horned and Long-eared Owls have ear tufts.

Barred owl *Strix varia*

http://earthobservatory.nasa.gov/Study/SpottedOwls/spotted_owls_6.html

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{an endangered species destroyed by gene flow!!!}
The dramatic expansion of the geographical range of coyotes over the last 90 years is partly explained by changes to the landscape and local extinctions of wolves, but hybridization may also have facilitated their movement.

We present mtDNA sequence data from 686 eastern coyotes and measurements of 196 skulls related to their two-front colonization pattern. We find evidence for hybridization with Great Lakes wolves only along the northern front, which is correlated with larger skull size, increased sexual dimorphism and a five times faster colonization rate than the southern front.

Northeastern haplotype mtDNA sequence diversity is low, suggesting that this population was founded by very few females moving across the Saint Lawrence. This northern front then spread south and west, eventually coming in contact with non-hybrid coyotes in western New York and Pennsylvania.

We suggest that hybridization with wolves in Canada introduced adaptive variation that contributed to larger size, which allowed eastern coyotes to better hunt deer, allowing a more rapid colonization of new areas than coyotes without introgressed wolf genes. ...
How to fail at species delimitation. Carstens et al. 2013 Molecular Ecology 22:4369

Six computer algorithms designed to infer phylogenetic relationships applied to 6 DNA loci from >24 populations

Salter et al. (2013)

Figure 1. Incongruent results from an empirical system. Six loci were used to delimit lineages in Aliatypus species complex, a group of trapdoor spiders from southern California (localities shown by dots in the inset map). Results from six methods (named at left) are depicted, with bars coloured to highlight congruence across methods. Numbers in parentheses represent the number of lineages delimited using each method. Also shown is an estimate of the species tree made using *Beast, with posterior probabilities shown under each node. Immediately above the species tree, thin coloured lines are used to identify the three species described by Satler et al. This figure is redrawn from Salter et al. (2013).

... the solution to the species problem is to treat the traditional criteria used to demarcate species as attributes that accumulate during the process of lineage diversification (de Queiroz 2005).
For some, species are simply the things you save; but for taxonomists, the concept is much more complex. Emma Marris asks whether Linnaeus's legacy is cut out for conservation.

Conservationists around the world were delighted to hear that the United States was considering adding polar bears to the list of animals enjoying the protection of the Endangered Species Act ...

But some experts may have greeted the news with a wry smile. Polar bears might well be threatened by the rapidly changing climate but whether they actually constitute a species is up for debate.

Genetic studies have shown that some brown bears (Ursus arctos) are more closely related to polar bears (U. maritimus) than they are to some other brown bears. According to some interpretations of the word species, this means that if brown bears are a species, then polar bears are not. {are they a DPS?}

... when modern taxonomy comes up against a conservation agenda, things can get very complex.
Emma Marris asks whether Linnaeus's legacy is cut out for conservation. 

Take a less iconic mammal ...

**Preble’s meadow jumping mouse** (*Zapus hudsonius preblei*).

It’s a threatened tea-cup-sized rodent with comically large feet and a counterbalancing tail, and spends its life hopping about the foothills of the Front Range in Colorado and Wyoming.

Or that’s how some would have it.

**Others say that the subspecies, is a spurious one, and that the creatures called by that name are just plain old meadow jumping mice** (*Zapus hudsonius*), a species with which the United States is crawling.

The streamside habitat preferred by the foothill mice is also prime real-estate land for development.

**The degree of protection accorded to the mice thus has implications for developers.**

... in 2005, the US Fish and Wildlife Service announced plans to drop Preble's mouse from its list of threatened species and subspecies because of new genetics work by Rob Ramey.

[another group] was commissioned to do further genetic tests. It disagreed with Ramey.

The agency called in an outside group; its verdict: the subspecies exists.
Emma Marris asks whether Linnaeus's legacy is cut out for conservation. Although it might be tempting just to see a story of evil developers and good conservationists, the mice highlight a more fundamental problem. The act includes in its definition of species ‘subspecies’ and ‘distinct population segments’ but offers no definitions for either of these categories. The reason why the relation between this mouse and that mouse can’t be nailed down with jurisprudential exactitude is the same reason that there are any mice in the first place: evolution. The problem is that the idea of a distinct species predates Darwin’s insights into their origins. Carl Linnaeus thought that species were made separate from one another by God, and that they stayed that way. But Darwin showed us otherwise. As one species splits into two over the millennia, there is no magic generation in which they are clearly separate. “It is kind of like asking when you are a child and when you are an adult - where is the boundary?”...
Emma Marris asks whether Linnaeus’s legacy is cut out for conservation.

The phylogenetic approach can ... call older taxonomy into doubt, as in the case of the polar and brown bears. ... studies of mitochondrial DNA suggest that brown bears do not share a common ancestor that does not also have polar bears as descendants; if you want to find one point on the tree from which all brown bears branch out, you will have to accept polar-bear branches in the same cluster. {next lect: brown bears not a proper “clade” ~ branch on tree of life; same problem with “reptiles” and birds}

By at least one reckoning, the phylogenetic approach comes up with 48% more species than the biological species concept does for the same group of organisms. “We are able to slice the genetic pie thinner and thinner,” says Craig Manson ...

Manson sees the Endangered Species Act as a creation of its time - a time when genetic data were still scarce ...

The act has no clear thresholds below which a group of organisms is not considered a unit for protection purposes.

“I think there needs to be a conference at the national level with the best experts in the scientific community that can be found, and let’s hear this issue,” says Manson. “
Emma Marris asks whether Linnaeus’s legacy is cut out for conservation.

The National Marine Fisheries Service ... shares the job of enforcing the Endangered Species Act ... and deals with the anadromous creatures - those that divide their lifecycle between salt and fresh water {salmon} ...

... of the ten listed populations ... on which most money is spent, eight are anadromous salmon or steelhead (rainbow trout).

Anadromous fish nearly always return to their natal stream to reproduce, and so fish from different streams ... are almost completely isolated when it comes to breeding.

So in the case of the chinook salmon (Oncorhynchus tshawytscha, which, as it happens, is considered by many to be the tastiest), those that spawn in the Columbia River basin are divided up into at least eight distinct population segments on the basis of their specific location and the timing of their runs. {which result in “phylogenetically distinct segments” w/ genetic differences}

Although there are many more than eight populations in the basin, their listing groups them together into units of a manageable size.

... the distinct population segment combines a biological description of the relationships with a value judgement as to whether a population is important.

“You really need something besides science to decide where on that level you are going to focus,” ...