Ecology and speciation

1) What are species

2) Reproductive isolation evolves with time

3) Spatial separation increases likelihood of speciation.

4) Speciation frequency increases with area

5) Speciation is driven by selection

6) Rapid speciation in postglacial fishes

7) Tests of ecological speciation

8) Speciation and sexual selection

9) Example exam questions
On the Origin of Species
by Means of Natural Selection,
or the Preservation of Favoured Races
in the Struggle for Life

Charles Darwin, M.A.,
Fellow of the Royal, Geological, Linnæan, etc. societies; Author of Journal of
researches during H.M.S. Beagle's Voyage round the world.
London: John Murray,
Albemarle Street, 1859

Introduction

WHEN on board H.M.S. Beagle, as naturalist, I was much struck with certain facts in the
distribution of the inhabitants of South America, and in the geological relations of the
present to the past inhabitants of that continent. These facts seemed to me to throw
some light on the origin of species; that mystery of mysteries, as it has been called by
one of our greatest philosophers. On my return home, it occurred to me, in 1837, that
something might perhaps be made out on this question by patiently accumulating and
reflecting on all sorts of facts which could possibly have any bearing on it. After five
years' work I allowed myself to speculate on the subject, and drew up some short notes;
these I enlarged in 1844 into a sketch of the conclusions, which then seemed to me
probable: from that period to the present day I have steadily pursued the same object. I
hope that I may be excused for entering on these personal details, as I give them to
show that I have not been hasty in coming to a decision.
1) What are species

Darwin’s definition of species

“I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other...”

“...the amount of difference is one very important criterion in settling whether two forms should be ranked as species or varieties.”

– Darwin (1859)
1) What are species

Biological species concept

Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups.

- Mayr (1942)

Speciation question: How does reproductive isolation evolve?
1) What are species

Reproductive isolation refers to evolved characteristics of populations that prevent gene flow, rather than geographic barriers.

Reproductive isolation need not be 100 percent (absolutely no gene flow) between species. Many, perhaps most, species hybridize to some degree with closely related species. Good species are “mostly” reproductively isolated.
Each dot in this figure indicates a pair of fly species or subspecies. The $y$-axis indicates the total amount of reproductive isolation between them. The $x$-axis indicates their genetic difference, reflecting their age.

The question is: how?

Coyne & Orr (2004) Speciation
3) Spatial separation increases likelihood of speciation

Young species tend to be spatially separated.

Older species tend to have greater overlap of geographic ranges.
Each dot in this figure is a Caribbean island. Speciation in *Anolis* lizards has taken place within islands only on the largest islands.

5) Speciation is driven by selection

“...the formation of isolating mechanisms entails building up of systems of complementary genes” – Dobzhansky (1937, 256)

Two populations initially genetically identical

Population 1

\[
\begin{array}{c}
\text{aa bb} \\
\text{mutation} + \\
\text{selection}
\end{array}
\]

\[
\begin{array}{c}
\text{Aa Bb}
\end{array}
\]

Population 2

\[
\begin{array}{c}
\text{aa bb} \\
\text{mutation} + \\
\text{selection}
\end{array}
\]

\[
\begin{array}{c}
\text{aa BB} \\
\text{X}
\end{array}
\]

The two populations accumulate genetic differences through time because of mutation and selection.

Eventually, these genetic differences cause individuals to avoid encountering/mating with one another,

or they cause problems in the hybrid offspring of individuals
Hypothesis of ecological speciation: reproductive isolation evolves as a by-product of divergent natural selection between environments.

Two populations in different environments

Divergent natural selection favors different alleles in each environment. Many such alleles cause incompatibilities, leading to speciation.
5) Speciation is driven by selection

Hypothesis of “mutation-order” speciation: reproductive isolation evolves as a by-product of fixation of different, incompatible mutations under similar selection pressures.

Two populations in similar environment

Population 1

Population 2

Selection pressures are similar on the two populations, but each population experiences and fixes unique mutations.

Many such alleles cause incompatibilities, leading to speciation.

This process is more sensitive to gene flow than is ecological speciation.
5) Speciation is driven by selection

The parallel evolution test supports the hypothesis of ecological speciation

Each dot in this figure estimates the probability of mating between two experimental fly populations raised separately for many generations either in the same environment or in different environments.

The red and blue dots are from two separate studies and experiments – both show the same pattern.

Repeatedly, more reproductive isolation has evolved between the populations in different environments compared to populations in similar environments.

Speciation is driven by selection
6) Rapid speciation in postglacial fishes

But does it happen in nature?
Tests using postglacial fishes

Northern N. America 13,000 years ago
6) Rapid speciation in postglacial fishes

Fish species at high latitudes tend to be younger, on average

Each dot in this figure is a pair of closely related fish species. The y-axis is genetic difference (reflecting age) and the x-axis is the midpoint of their latitudinal ranges.
6) Rapid speciation in postglacial fishes
   Even younger species are found in some postglacial bodies of water
7) Tests of ecological speciation

Try the parallel evolution test

We can use the same test as in the laboratory experiments on flies. Compare the amount of reproductive isolation between populations that have experienced similar versus different selection pressures.
7) Tests of ecological speciation

Lab mating trials using wild-caught fish
7) Tests of ecological speciation

The parallel speciation test with stickleback

Each dot in this figure estimates the probability of mating between two stickleback populations inhabiting either the same environment or different environments.

Repeatedly, more reproductive isolation has evolved between populations in different environments than between populations in similar environments.
7) Tests of ecological speciation

Trait-based assortative mating test

A second prediction of ecological speciation is that assortative mating should depend on differences in traits that evolved by divergent natural selection.
7) Tests of ecological speciation

Probability of hybridizing depends on body size

Each dot in the plot indicates the body sizes (length) of male and female fish that were paired during mating trials. The filled dots indicate trials that resulted in spawning; open dots indicate no spawning. The dotted lines indicate size equality, \( Y=X \)
7) Tests of ecological speciation

Trait-based assortative mating test

*Mimulus lewisii*
- bee-pollinated
- pink flowers
- wide corolla
- small volume of nectar
- inserted anthers and stigma
- petals thrust forward to provide a landing platform
- two yellow ridges of brushy hairs (nectar guides)
- wet habitats between 1600m and 3000 m

*M. cardinalis*
- hummingbird-pollinated
- red flowers
- narrow tubular corolla
- a large nectar reward
- exserted anthers and stigma to contact hummingbird forehead
- reflexed petals
- wet habitats from sea level to 2000 m

Schemske & Bradshaw (1999) PNAS
Despite striking morphological differences, the two monkeyflower species are very closely related.

The floral traits that confer pollinator specificity (bee vs hummingbird) also contribute to premating reproductive isolation.

Schemske & Bradshaw (1999) carried out a field experiment to investigate what floral traits caused pollinator discrimination and the genetic basis of the traits. They used genetic markers to determine the genetic basis of pollinator visitation.
7) Tests of ecological speciation

The researchers generated F2 hybrids in the lab in Seattle, creating an experimental population in which different traits varied more or less independently.

They transported the plants in pots to plots in Yosemite National Park where the field experiment was carried out.

They then correlated the visitation rates by bees and by hummingbirds to characteristics of the F2 plants.

Schemske & Bradshaw (1999) *PNAS*
Pollinators choose based on the traits that most differentiate the flowers of the two species.

These traits thus contribute to assortative mating between the species.

Schemske & Bradshaw (1999) *PNAS*
Near-isogenic lines of *M. lewisii* and *M. cardinalis* with alternate alleles at the YUP locus. The wild-type allele at the YUP locus (left) has been substituted by introgression with the allele from the other species (right).

In this follow-up experiment the authors showed that moving one gene, YUP, from one species to the other had substantial effects on pollinator preference and thus could affect reproductive isolation.


<table>
<thead>
<tr>
<th></th>
<th>Bees (visits per 1000 flowers per hour)</th>
<th>Hummingbirds (visits per 1000 flowers per hour)</th>
</tr>
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<tbody>
<tr>
<td><em>lewisii</em></td>
<td></td>
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<tr>
<td>Wild type (pink)</td>
<td>15.4</td>
<td>0.02</td>
</tr>
<tr>
<td>Mutant (yellow-orange)</td>
<td>2.63</td>
<td>1.44</td>
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<tr>
<td><em>cardinalis</em></td>
<td></td>
<td></td>
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<tr>
<td>Wild type (red)</td>
<td>0.15</td>
<td>189</td>
</tr>
<tr>
<td>Mutant (dark pink)</td>
<td>10.9</td>
<td>168</td>
</tr>
</tbody>
</table>
7) Tests of ecological speciation

Direct selection test

A third prediction of ecological speciation is that ecologically based natural selection directly reduces gene flow by acting against immigrants and/or hybrids.

1. Ecologically based selection against migrants. In many species mating can only take place between individuals living near one another. Selection against migrants reduces opportunities for matings between populations.

2. Ecologically based selection against migrants. The fitness of hybrids is reduced in one or both the environments of the parent species, whereas in the lab the hybrids do fine.

Example: Sympatric races of pea aphids on alfalfa and red clover are highly ecologically specialized and significantly reproductively isolated.
7) Tests of ecological speciation

Direct selection test

Aphids transplanted between the two host plants have low fitness. Each type has difficulty feeding on the other’s plant. This directly reduces the opportunity for interbreeding between the host races, and so contributes to reproductive isolation. F1 hybrids also have reduced fitness on both host plants for similar reasons.

Performance of winged pea aphids after simulated migration to either alfalfa or clover. Aphids collected from alfalfa (open bars) and red clover (solid bars) were moved from the home plant to the test plant on the second day of adulthood, consistent with the timing of naturally occurring flight. (A) Fecundity in the 21 days after migration. (B) Percent of individuals surviving through the entire 21-day experiment.

Via et al (2000) *Evolution*
The combined contribution of trait-based assortative mating and direct selection to total reproductive isolation between ecologically-differentiated plant and animal species and subspecies in nature is often substantial, as the figure below illustrates.

Schluter (2009) Science
Many differences between the closely related species are in traits seemingly unrelated to ecology, such as color, song, gamete recognition.

Evidently, the speciation process often involves the evolution of traits involved in mate choice/recognition, which implicates sexual selection.

But how?
8) Speciation by sexual selection

The key to understanding the role of sexual selection in speciation seems to be understanding the forces driving the rapid evolution of the preferences, since the preferences drive the evolution of sexually-selected traits.

Preferences might evolve rapidly for at least two reasons:

1. The preferences evolve by natural selection on the sensory system.

2. Conflict between the sexes, which drives continual adaptation in one sex and counter-adaptation in the other.

We don’t know very much about either of these processes.
8) Speciation by sexual selection

Sexual conflict has been suggested as the process driving the extremely rapid evolution of gamete recognition proteins observed in some groups of broadcast-spawning marine invertebrates, such as shallow water sea urchins, abalone, mussels and snails.

When sperm concentrations are high, multiple sperm entry into eggs — polyspermy — can kill developing embryos. The conflict hypothesis is that when the risk of polyspermy is high, an allele at an egg surface protein gene is favored that slows sperm entry. Fixation of such an allele would create evolutionary pressure on sperm proteins to evolve more efficient egg entry. The cycle could ultimately lead to lack of recognition of sperm and eggs from different populations, i.e., reproductive isolation.
8) Speciation by sexual selection

In contrast, work on this pair of Lake Victoria cichlid fishes provides evidence that natural selection on the sensory system is driving divergence and reproductive isolation. This is ecological speciation but involving sexual selection.

`blue’, typical *P. pundamilia*

`red’, typical *P. nyererei*

8) Speciation by sexual selection

Low wavelength (blue) light doesn’t penetrate very deep in Lake Victoria, so light at greater depths is red-shifted. Blue objects look brown at even moderate water depths. In areas of clear water and moderate depth gradients, both species are found. The blue species lives in the shallower water, the red species at depth.

The two species have different long-wave sensitive pigments in the eye (opsins) that affect color vision. The pigment of the red species is more red-shifted.
Ecology and speciation

The evidence suggests that natural selection drives the origin of new species, as Darwin claimed.

Evidence support the ecological hypothesis of speciation in many systems. Reproductive isolation often evolves as a consequence of adaptation to contrasting ecological environments.

Natural selection might also lead to divergence by the “mutation-order” mechanism, in which each population adapts by a unique series of mutations. We didn’t talk much about this, but there are examples involving intragenomic conflict (e.g., nuclear - mitochondrial).

Sexual selection may be an important component of speciation by ecological (e.g., adaptation of sensory system to environment) and mutation-order (e.g., sexual conflict) mechanisms.

Other mechanisms are also known to be involved in speciation, such as hybridization and polyploidy, which we haven’t discussed. There is continuing interest in the possibility of speciation by genetic drift, but evidence is wanting.
9) Example exam questions

What is a species, according to the biological species concept?

Distinguish briefly: ecological speciation and mutation-order speciation.

Provide an explanation for why speciation occurs more frequently in larger geographic areas than in smaller areas.

A new pair of herbivorous insect species is discovered on a group of islands. On each island, one species utilizes *Abutilon* as its host plant, whereas the other uses *Scalesia*. Phylogenetic evidence suggests that each island pair evolved independently. Design one experiment to test whether the pairs evolved via ecological speciation.

Suggest a mechanism by which sexual conflict might lead to the evolution of reproductive isolation between populations.