Coevolution

- Fitness is a genotype-by-environment interaction.
- The environment for one species includes other species.
- For species that interact, they form part of each other’s “environment.”
- As one species adapts to the “environment” defined by the other species, the other species in turn can adapt to the changing “environment” created by evolution in the first species.
- Interactions between species therefore can set up an evolutionary feedback loop that causes the species to COEVOLVE in response to one another.

Coevolution is simply natural selection operating within each of the interacting species, recognizing that each species constitutes part of the environment of the other species.
**Interspecific Interactions**

<table>
<thead>
<tr>
<th>Species 1</th>
<th>Species 2</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>Neutralism</td>
</tr>
<tr>
<td>+</td>
<td>0</td>
<td>Commensalism</td>
</tr>
<tr>
<td>-</td>
<td>0</td>
<td>Amensalism</td>
</tr>
<tr>
<td>+</td>
<td>-</td>
<td>Predator-prey; Herbivore-plant Pathogen-host</td>
</tr>
<tr>
<td>-</td>
<td>-</td>
<td>Competition</td>
</tr>
<tr>
<td>+</td>
<td>+</td>
<td>Mutualism</td>
</tr>
</tbody>
</table>

**True Interactions**

**E.g., Heliconius Butterflies**

- **Same Species In Different Areas**
- **Different Species In The Same Area**
Mimicry rings show convergent and divergent evolution within Heliconius.

Passiflora caterpillars feed on passiflora, which makes them poisonous to birds. They evolve warning coloration. Experiments show that bird predators can quickly learn to avoid these color patterns, but this learning is more rapid when all butterflies in a single area converge upon a common pattern. This type of mutualistic mimicry is called Müllerian mimicry.
Coevolutionary interactions among species can be complex; e.g., *Heliconius* butterflies are very long-lived as adults and reproduce throughout that long life. Therefore, they need a pollen source for proteins. The species are involved in intense competition for these pollen resources.

*Heliconius cydno* gathers pollen from *Psiguria* flower.
(Rainforest cucumber)

Different *Heliconius* species lay eggs on different species of *Passiflora*:
are neutralists for larval food resources.
Different *Heliconius* species use the same pollen food resources: Hence their adult foraging behaviors are driven by competitive interactions.

Different *Heliconius* species are selected to converge upon a common, mutualistic warning coloration pattern by their interspecific interaction with birds.
Different traits within the same species can coevolve in radically different directions. Mendelian genetics allows such complex coevolution to occur.

Mendelian genetics allows such complex coevolution to occur in part because underlying genetics is simple.

Kronforst *et al.* (Genetics 174:535-539, 2006) did a genome scan using some of the most divergent species in genus. Found that different species achieved phenotypic convergence via homologous genes, and only 9 genes can explain the amazing wing diversity in this group.
optix expression prefigures red wing patterns in *Heliconius*

R D Reed et al. Science 2011;333:1137-1141

In Some Cases, the Simple Mendelian Units of Selection Are Actually Evolved Supergenes; e.g., the P supergene in *H. numata*.

BP1 and BP2 are rearrangements from the ancestral state that suppress crossing-over

silvana haplotypes behave as dominant alleles over aurora haplotypes with respect to wing pattern. aurora haplotypes found in silvanta individuals were all in s/a heterozygotes.


An Early Answer To This Was Pleistocene Refuges: the idea that climatic fluctuations in the Pleistocene created isolated subpopulations which adaptively diverged to form the initial “races”. Modern studies fail to support the existence of these refuges and modern comparative analysis indicate that the divergence times are not consistent with climatic fluctuations.

A second idea was that *Heliconius* species show strong population subdivision, and genetic drift interacting with selection (e.g., shifting balance) created differences among local populations leading to “races”. But modern population genetic studies indicate that most species of *Heliconius* are strong dispersers marked by much gene flow and little population subdivision.


They examined the fine-scale population genetic structure of eight Costa Rican *Heliconius* species with 1428 AFLP markers. The species were chosen from two clades: molecular phylogenetics indicates that one clade was the first to diversify into local “races”, and the second clade evolved later to parallel the first group through coevolution.

3 of the 4 species in the older clade show significant isolation by distance, and the most abundant species (*H. erato*), which should dominate much of the coevolution, has a large $f_{st}$, indicating a strong potential for drift and shifting balance.
Kronforst and Gilbert (2008, Proceedings of the Royal Society B: Biological Sciences 275:493-500) suggest an alternative. The species in the clade that later radiated onto these patterns had intermediate levels of genetic diversity and less genetic differentiation among populations.

Only 1 of the 4 species in the younger clade show significant isolation by distance: little potential for drift and shifting balance.

Genetic Drift in perhaps just one, widespread, abundant but highly subdivided species triggered adaptive local differentiation in other species through coevolution that did have the population structure to initiate such differentiation.

MALLET, J., (2010 Shift happens! Shifting balance and the evolution of diversity in warning colour and mimicry. Ecological Entomology 35: 90-104) supports this alternative, arguing that the most highly subdivided species, H. erato, drives the mutualistic coevolutionary system.