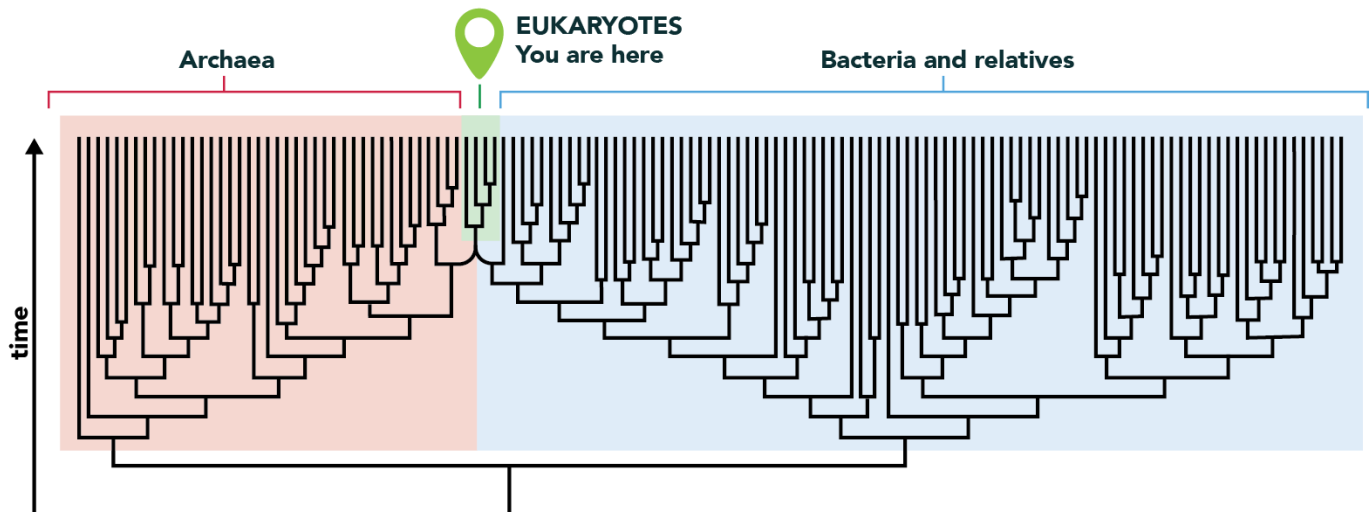## Macroevolution

Macroevolution is evolution on a grand scale — what we see when we look at the over-arching history of life: stability, change, lineages arising, and extinction.
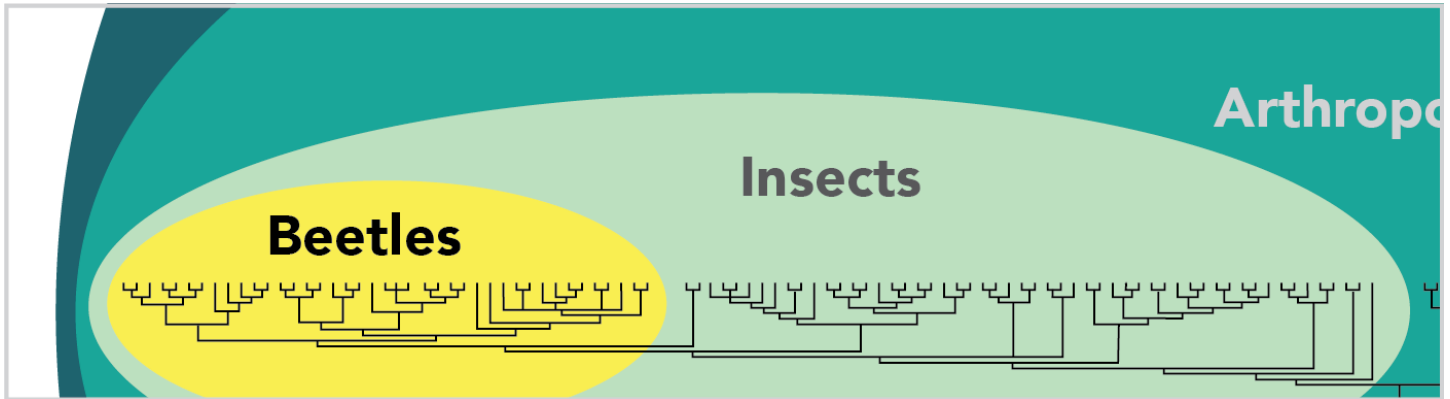

Tree of Life adapted from Hug et al. (2016)

Here, you can examine the patterns of macroevolution in evolutionary history and find out how scientists investigate deep history.

What is macroevolution?

Macroevolution generally refers to evolution above the species level. So instead of focusing on an individual beetle species, a macroevolutionary lens might require that we zoom out on the tree of life, to assess the diversity of the entire beetle clade and its position on the tree.

Macroevolution refers to evolution of groups larger than an individual

Macroevolution encompasses the grandest trends and transformations in evolution, such as the origin of mammals and the radiation of flowering plants. Macroevolutionary patterns are generally what we see when we look at the large-scale history of life.

It is not necessarily easy to "see" macroevolutionary history; there are no firsthand accounts to be read. Instead, we reconstruct the history of life using all available evidence: geology, fossils, and living organisms.

Once we've figured out *what* evolutionary events have taken place, we try to figure out *how* they happened. Just as in microevolution, basic evolutionary mechanisms like mutation, migration, genetic drift, and natural selection are at work and can help explain many large-scale patterns in the history of life.

The basic evolutionary mechanisms — mutation, migration, genetic drift, and natural selection — can produce major evolutionary change if given enough time.

A process like mutation might seem too small-scale to influence a pattern as amazing as the beetle radiation, or as large as the difference between dogs and pine trees, but it's not. Life on Earth has been accumulating mutations and passing them through the filter of natural selection for 3.8 billion years — more than enough time for evolutionary processes to produce its grand history.
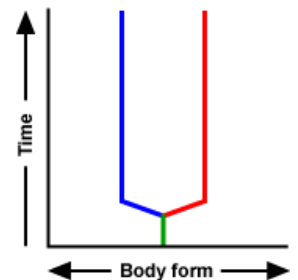
Patterns in macroevolution

You can think of patterns as "what happened when." All of the changes, diversifications, and extinctions that happened over the course of life's history are the patterns of macroevolution.
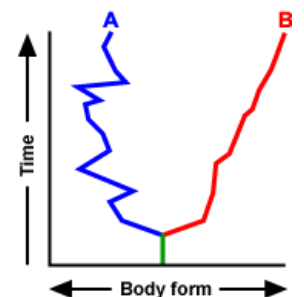
However, beyond the details of individual past events — such as, when the beetle radiation began or what the first flowers looked like — biologists are interested in general patterns that recur across the tree of life:

1. **Stasis:** Many lineages on the tree of life exhibit stasis, which just means that they don't change much for a long time, as shown in the figure to the right. In fact, some lineages have changed so little for such a long time that they are often called living fossils. Coelacanths comprise a fish lineage that branched off of the tree near the base of the vertebrate clade. Until 1938, scientists thought that coelacanths went extinct 80 million years ago. But in 1938, scientists discovered a living coelacanth from a population in the Indian Ocean that looked very similar to its fossil ancestors. Hence, the coelacanth lineage exhibits about 80 million years' worth of morphological stasis.
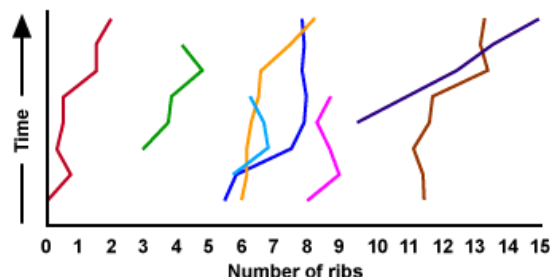

A coelacanth swimming near Sulawesi, Indonesia. Photo courtesy of Mark V. Erdmann.

2. **Character change:** Lineages can change quickly or slowly. Character change can happen in a single direction, such as evolving additional segments, or it can reverse itself by gaining and then losing segments. Changes can occur within a single lineage or across several lineages. In the figure to the right, lineage A changes rapidly but in no particular direction. Lineage B shows slower, directional change. Trilobites, animals in the same clade as modern insects and crustaceans, lived over 300 million years ago. As shown below, their fossil record clearly suggests that several lineages underwent similar increases in segment number over the course of millions of years.
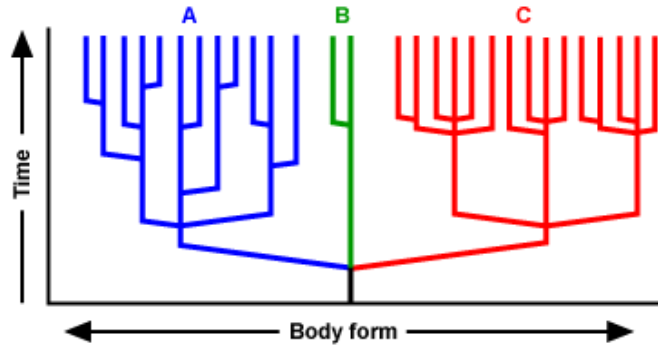

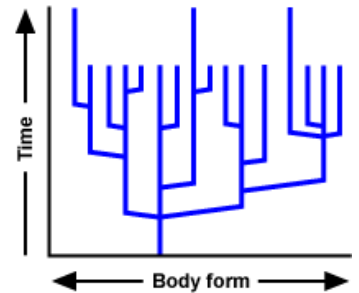Changes in the number of ribs across eight trilobite lineages

3. **Lineage-splitting** (or speciation): Patterns of lineage-splitting can be identified by constructing and examining a phylogeny. The phylogeny might reveal that a particular lineage has undergone unusually frequent lineage-splitting, generating a "bushy" tuft of branches on the tree (Clade A, below). It might reveal that a lineage has an unusually low rate of lineage-splitting, represented by a long branch with very few twigs coming off (Clade B, below). Or it might reveal that several lineages experienced a burst of lineage-splitting at the same time (Clade C, below).

4. **Extinction:** Extinction is extremely important in the history of life. It can be a frequent or rare event within a lineage, or it can occur simultaneously across many lineages (mass extinction). Every lineage has some chance of becoming extinct, and overwhelmingly, species have ended up in the losing slots on this roulette wheel: over 99% of the species that have ever lived on Earth have gone extinct. In this diagram, a mass extinction cuts short the lifetimes of many species, and only three survive.

Patterns in macroevolution

Extinction is a fact of the history of life. Just as new lineages have evolved over Earth's history, so, too, have lineages gone extinct. This balance of speciation and extinction has generated turnover in the set of species alive at each point in time. Biologists have long wondered if there are patterns in this churning of biodiversity. In particular, are there factors that predispose a species to extinction? Answering this question has taken on urgency as we face what is shaping up to be the Earth's 6th mass extinction, caused not by meteorite impacts or volcanic activity, but by humans. If we could figure out which species are most vulnerable to extinction, perhaps we could work out better ways to protect them.

Melissa Kemp, Assistant Professor at the University of Texas at Austin, excavating a cave site in the Caribbean. Photo provided by Melissa Kemp.

Biologists have already found that large body size is a risk factor for extinction. Several intuitive hypotheses could explain this. Larger organisms often reproduce more slowly, producing fewer offspring and taking longer to mature, so they can't bounce back as quickly if their numbers are reduced. Larger organisms also often have smaller population sizes to begin with and require a larger home range to sustain those populations, putting them at risk of extinction if part of that range is made uninhabitable. This pattern (increased risk of extinction with larger body sizes) has been observed in several different animal groups. For example, among living bird species, birds with larger bodies are more likely to be at higher risk of extinction. Biologists Melissa Kemp and Elizabeth Hadly wondered if it might also hold true for lizards in the Caribbean, a biodiversity hotspot, over the last few million years. **Are larger body sizes associated with greater risk of extinction in Caribbean lizards?**

Liz Hadly, Professor at Stanford University, in Nepal while doing fieldwork on Pikas. Photo by Uma Ramakrishnan.
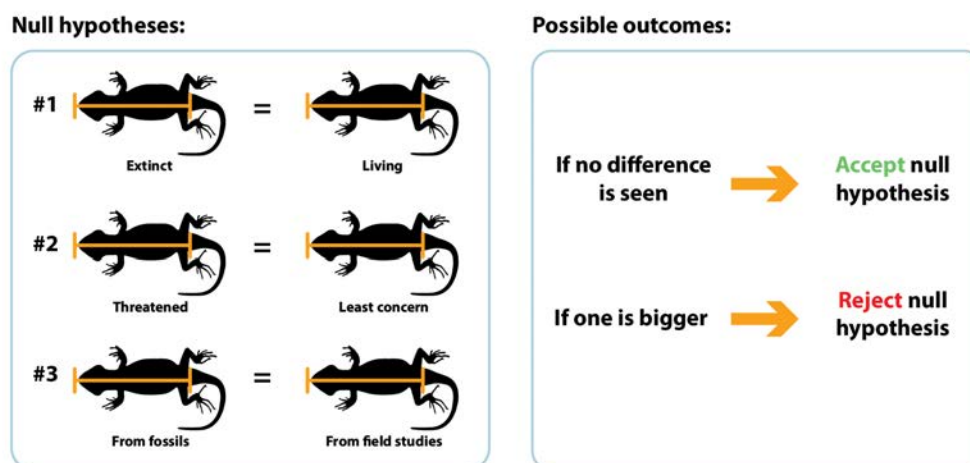
Hypotheses

Melissa and Liz investigated their question using statistical tests that rely on a null hypothesis. A null hypothesis proposes that there is *no* difference or *no* association between variables. If your statistical tests rejects the null hypothesis, then you know that the patterns in the data are not due to chance alone and are likely meaningful. Hence, the team's null hypotheses were:
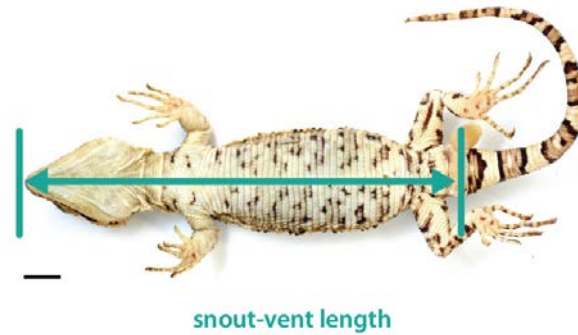
1. **Extinct Caribbean lizard species have the same distribution of body sizes as living Caribbean lizard species.** Larger species are not particularly likely to have gone extinct over the last 2.6 million years.

2. **Among modern Caribbean lizards, threatened species have the same distribution of body sizes as those not at risk of extinction (i.e., species of "least concern").** Among modern species, larger species are not particularly likely to be at elevated risk of extinction.Testing these null hypotheses required comparing data from modern lizard species to data from fossils. However, this introduced a potential bias to the study. What if larger or smaller species are more likely to show up in the fossil record? That could cause a pattern in the data – one that Melissa and Liz might mistake for extinction bias, when it was really preservation bias (which species are more likely to fossilize). To rule out this possibility, Melissa and Liz needed to check one more null hypothesis:

3. **Caribbean lizard species known from fossils have the same distribution of body sizes that those known from modern-day field studies.** Fossilization is not size-biased.
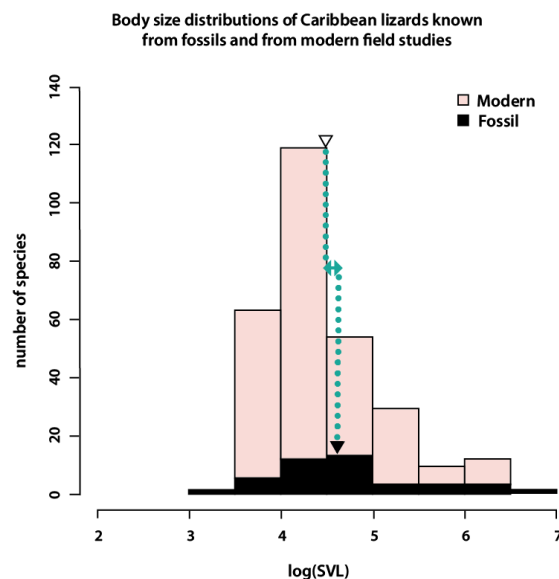
This table summarizes all three null hypotheses:

Data

To test their hypotheses, Melissa and Liz needed a lot of data on body size in both modern and ancient Caribbean lizards, as well as information about which species went extinct and which are currently threatened with extinction. Luckily, a lot of these data had already been collected by other researchers. Melissa and Liz put together their data set from previously published studies, estimating the body size of extinct lizards from the sizes of fossilized bones and closely related modern species. Body size was indicated by the distance between the tip of a lizard's snout and its cloacal slit – aka, the snout-vent length (SVL). To make patterns in the data easier to see and work with, they use math to transform the data. Specifically, they took the log of the SVL for all their lizard species. This changes the magnitude of each data point, but keeps the relationships among data points the same (e.g., the largest raw number is still the largest after log-transformation). They divided modern species into "threatened" or "non-threatened" based on their conservation status according to the IUCN (International Union for Conservation of Nature) Red List.
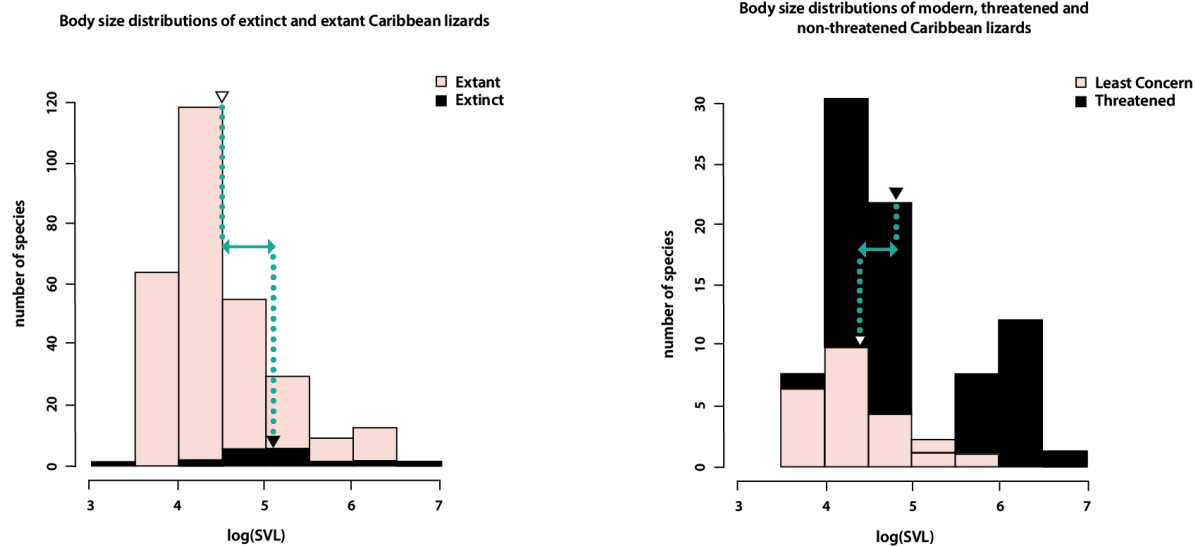
snout-vent length

Testing null hypothesis 3 – Do species known from fossils have the same range of sizes as species known from modern field studies? Though this question was not the main point of the study, knowing its answer would be key in interpreting the data for null hypothesis 1.

Body size distributions of Caribbean lizards known from fossils and from modern field studies

It's clear from this graph (and its much longer pink bars) that there are lots more species known from modern field studies than from studies of fossils. But does one group tend to have *larger* species than the other? Body size is shown on the x-axis. The triangles in the graph above represent the mean log body size for each group, and they appear to be similar (see blue annotation). Statistics can tell us if that small difference is likely a meaningful pattern or one that could easily be due to chance alone. Melissa and Liz performed a Kolmogorov-Smirnov test, which calculates the likelihood that two samples come from the same underlying distribution (i.e., are statistically "the same"). The *p*-value was 0.11, indicating that 11% of samples drawn from the same distribution would differ by this much or more just by chance alone. The usual cut-off for a significant difference is 5%, so they did *not* reject this null hypothesis, meaning that the small differences between the size of modern and fossil species in this sample could easily be caused by chance alone and not by a true difference between the overall sizes of the groups. In other words, fossilization does not appear to be size-biased in this group. That meant that whatever patterns Melissa and Liz found while investigating their other hypotheses are likely to represent real differences in body size and extinction risk.

Testing null-hypotheses 1 and 2 – Do extinct and threatened species have the same distribution of body sizes as living and "least concern" species?

Body size distributions of extinct and extant Caribbean lizards

Body size distributions of modern, threatened and non-threatened Caribbean lizards

In these graphs, the triangles again represent the mean log body size of each group. At left, in the blue annotation, we can see that extinct species tend to have larger body sizes than extant (living) species. At right, we can see that threatened species tend to have larger body sizes than species of least concern. Are these differences significant? Melissa and Liz's statistical tests showed that they are. Fewer than one in a thousand samples drawn from the same distribution would have had the observed or greater size differences between extinct and extant species ($p < 0.001$) by chance alone. And fewer than three in a thousand samples would have had the observed or greater size differences between threatened and least concern species ($p < 0.003$) by chance alone. This means that it is extremely *un*likely that the observed size differences occurred by chance alone, and much *more* likely that there were true differences between the two sample sets. The researchers' data led them to reject both of their other null hypotheses: extinct Caribbean lizard species are larger than living Caribbean lizard species, and threatened Caribbean lizard species *are* larger than "least concern" Caribbean lizard species.

This is yet another line of evidence suggesting that body size matters when it comes to extinction – larger Caribbean lizard species are more likely to have gone extinct in the past and are more likely to be threatened or endangered today. What we still don't fully understand, however, is *why*? Do large, slow-reproducing lizard species evolve slowly and so don't adapt to environmental changes as efficiently as smaller species? Is it that they require larger home ranges and are more vulnerable to extinction via habitat loss? Answering these questions will shed even more light on what we can do to optimize our conservation efforts.

Stepping into science

Melissa loves to paint and draw. She thought she would grow up to be an artist. Today she finds that the approaches that informed her art – her appreciation for nature, perseverance, and eye for detail – make her a better scientist too! Liz didn't set out to be a scientist either. She had never had a science or math teacher who was a woman, so couldn't picture having that job. Now she's the role model she didn't have as a girl!