Adaptive Radiation

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The diversity of life on Earth is governed, at the **MACROEVOLUTIONARY** scale, by two antagonistic processes: *Evolutionary radiations* increase and *extinction events* decrease the organismal diversity on our planet through time. Evolutionary radiations are termed *adaptive radiations* if new lifeforms emerge rapidly through the extensive ecological diversification of an organismal lineage.

MACROEVOLUTION
Evolution on the grand scale, that is, evolution at the level of species and above.

ECOLOGICAL NICHE
The relational position of a species or population in an ecosystem. It includes the interactions of all biotic and abiotic factors that determine how a species meets its needs for food and shelter, how it survives, and how it reproduces.

FOSSIL
Any preserved evidence or traces of life from a past geological era, such as impressions and remains of organisms embedded in rocks or in marine or lake sediments, or mineralized bones or plant material.

CAMBRIAN EXPLOSION
(also known as "Cambrian evolutionary radiation")
An evolutionary event in the Cambrian period, documented in the fossil record (*e.g.*, in the Burgess shale), during which most of the animal phyla emerged within a relatively short period of time.

Examples of adaptive radiations

Adaptive radiation refers to the evolution of ecological and morphological disparity within a rapidly diversifying lineage. It is the diversification of an ancestral species into an array of new species that occupy various **ECOLOGICAL NICHES** and that differ in traits used to exploit those niches. Adaptive radiation includes the origination of both new species (speciation) and phenotypic disparity.

Archetypal examples of adaptive radiations include Darwin's finches on the Galápagos archipelago; silversword plants on Hawaii; anole lizards on the islands of the Caribbean; threespine stickleback fish in north temperate waters; and cichlid fishes in the East Africa Great Lakes and in various tropical crater lakes (see **FIGURE 1**). Adaptive radiations are also visible in the **FOSSIL** record. For example, the **CAMBRIAN EXPLOSION** is considered an adaptive radiation.

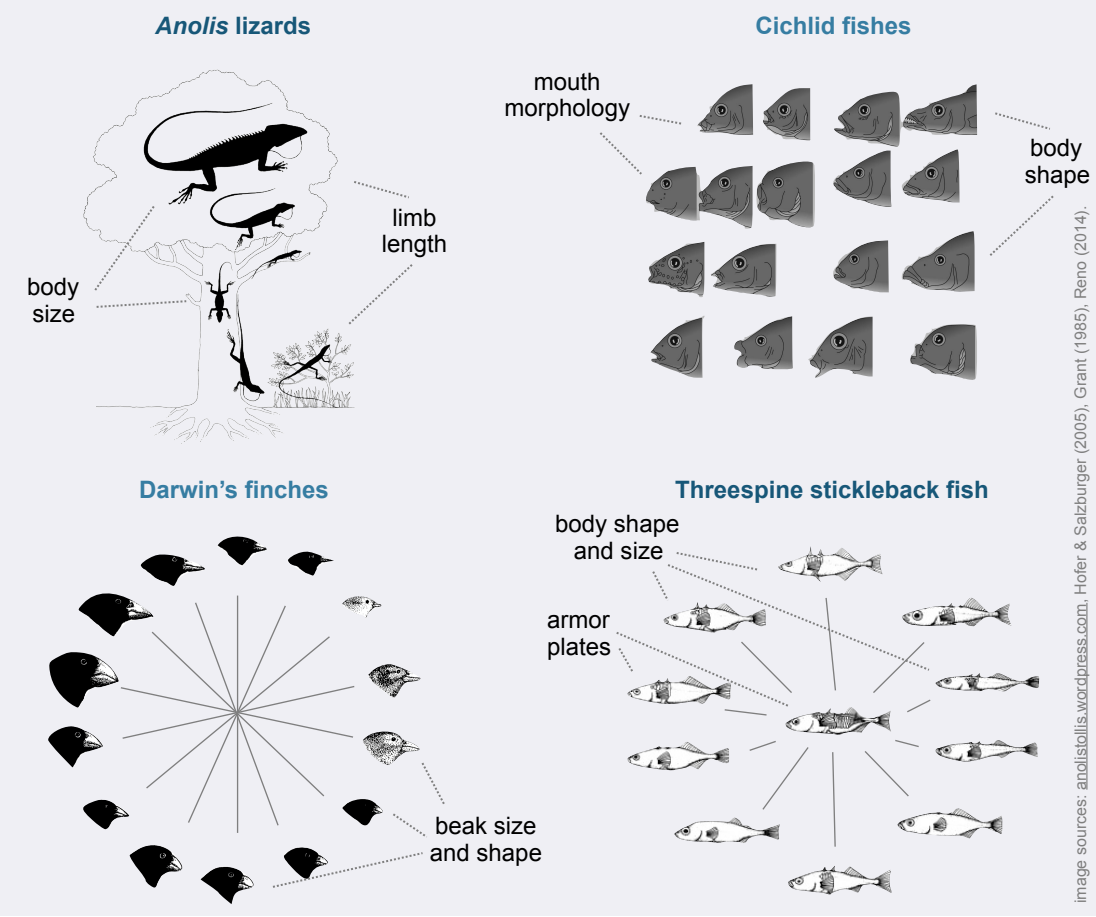

FIGURE 1. *Famous examples of ongoing vertebrate adaptive radiations and examples of adaptive traits in the respective radiation.*

Characteristic features of an adaptive radiation

ENVIRONMENT The surroundings in which a species lives and operates, including all of the biotic and abiotic factors that affect the survival and development of an organism or population.

An adaptive radiation is defined by four characteristic features, which are also used to detect instances of adaptive radiations (see Schluter 2000):

1. *Common ancestry*: Members of an adaptive radiation are characterized by their common ancestry, that is, all species of an adaptive radiation go back to a single common ancestor. Common ancestry is not the same as monophyly, as not *all* descendants of the common ancestor need to be included in the radiation.
2. *Phenotype-environment correlation:* In an adaptive radiation, there is a fit between the diverse phenotypes of the descendant species and the divergent **ENVIRONMENTS** in which they live. For example, the body and limb size of *Anolis* lizards matches the twig diameter in their habitat (see **FIGURE 1**). **BOX 1** provides further example of phenotype-environment correlations.
3. *Trait utility:* The morphological and/or physiological traits that differ between the descendant species of an adaptive radiation are "useful" to exploit the respective ecological niche. For example, the different bills of Darwin's finches are useful for a particular food type.
4. *Rapid speciation:* In an adaptive radiation, speciation is typically rapid. Speciation during adaptive radiation can be allopatric, but is primarily parapatric or sympatric, as adaptive radiations are, in most cases, confined to a certain geographic area.

BOX 1: **Examples of adaptive radiation** and the associated phenotype-environment correlations (modified from Schluter 2000).

Taxon	Region	Phenotype-environment correlation	Trait Performance
Animals			
Darwin's finches *(Geospiza)*	Galápagos	bill size and shape - seed size and seed hardness	handling time; breaking stress; crushing force
Crossbills *(Loxia)*	North America	bill size - cone strength, cone stage	handling time
Tits *(Parus)*	Eurasia	body size and limb length - substrate; bill shape - habitat	foraging ability; hanging and perching ability
Caribbean lizards *(Anolis)*	Greater Antilles	body size and hindlimb length - perch diameter and hight	sprint speed; jump distance; running stability
Sunfishes *(Centrarchus)*	North America	bod size and gape - prey size; pharyngeal jaw musculature - snail	handling time; crushing force
Stickelback fish *(Gasterosteus)*	Northern hemisphere	body size - prey size; body shape - habitat	foraging success; growth rate
Lake whitefish *(Coregonus)*	Northern hemisphere	gill rakers - habitat	foraging ability
Cichlid fishes (Cichlidae)	Southern hemisphere	premaxilla angle and length - diet pharyngeal jaw bone - diet	biting and suction force
Plants			
Coumbines *(Aquilegia)*	North America	flower orientation - pollinators; spur length, color - pollinator	pollinator visits; pollen removal
Brittlebush *(Encelia)*	North America	pubescence - temperature, moisture regime	transpiration, photosynthesis
Silverswords *(Dubautia)*	Hawaii	tissue elastic modulus - habitat	turgor pressure
Orchids *(Ophrys)*	Mediterranean	flower morphology, color, flowering time - pollinator	pollination success

Triggers of adaptive radiation

An adaptive radiation can occur under a number of different circumstances, which have in common that they create **ECOLOGICAL OPPORTUNITY** for the subsequent radiation to occur:

1. *Colonization of a new area*: Many adaptive radiations occurred after an ancestral species colonized a new area in which the adaptive radiation takes place (*e.g.*, the Galápagos archipelago in case of Darwin's finches, the Hawaiian islands in case of *Drosophila* or silversword plants, the islands of the Caribbean in case of *Anolis* lizards, and various small and large lakes in case of cichlid fishes). Adaptive radiations are often connected with the emergence of novel (empty) habitats such as islands or lakes. Such newly colonized areas are typically characterized by reduced predation pressures and competition on the one hand, and un- or underexploited **RESOURCES** on the other hand.
2. *Extinction or replacement of antagonists:* An adaptive radiation may occur after competitors become extinct or get replaced. That way, ecological niches that were previously occupied by other taxa become vacated. Here, extinction refers to a rapid (cataclysmic) process, whereas replacement refers to a more gradual process, for example due to environmental change.
3. *Adaptive breakthrough*: An adaptive radiation may be initiated by the evolution of a new adaptive trait that allows a taxon to outcompete other taxa or to exploit previously underutilized resources. **EVOLUTIONARY INNOVATIONS** are termed "*key innovations*" if they are responsible for an adaptive radiation. Examples of key innovations are the Antifreeze glycoproteins in Antarctic notothenioid fish ('icefishes') allowing them to survive in the ice-cold waters off Antarctica or the nectar spurs in the flowers of columbine plants leading to a strong associated between plant species and pollinator.

ECOLOGICAL OPPORTUNITY
The environmental conditions that permit the persistence of an evolutionary lineage.

RESOURCES
A substance or object in the environment required by an organism for growth, maintenance, and reproduction. Resources can be *exploited* (consumed) and thus become unavailable.

EVOLUTIONARY INNOVATION
Lineage-restricted trait with a qualitatively new function, such as feathers in birds or the flower of flowering plants.

MASS EXTINCTION
An extinction event during which more than three-quarters of all species on our planet disappear in a geologically short time interval.

Extinction

The history of life can be viewed as a cumulative story of evolutionary, often adaptive, radiations, interrupted by extinction events (on top of the more or less gradual processes of speciation and small-scale extinction). The fossil record documents past radiations and extinctions, but is by no means complete. This is because the long-term preservation and subsequent discovery of fossils is an extremely rare event; fossil remains are usually incomplete or damaged; the fossilization process requires specific settings and conditions, so that fossils are typically restricted to particular environmental settings (such as caves, sediments, deserts); finally, the fossil record is heavily biased towards organisms with hard parts such as mollusks or vertebrates, whereas fossils of soft-bodied organisms are only rarely to be found.

Extinction is a common process in evolution and it is believed that 99% of all species that ever existed since the dawn of life on Earth about 3.5 billion years ago have meanwhile gone extinct. However, extinction is normally balanced out by speciation (and radiation). The fossil record (primarily the one in the marine realm) nevertheless documents five **MASS EXTINCTION** events (see **Box 2**). Some scientists believe that a sixth such event is currently ongoing.

Box 2: **The 'big five' mass extinction events** (modified from Barnosky *et al.* 2011).

Event	**end point**	**duration**	**% genera lost** (estimate)	**% species lost** (estimate)
Ordovician event	ca. 443 My ago	3.3 - 1.9 My	57	86
Devonian event	ca. 359 My ago	29 - 2 My	35	75
Permian event	ca. 251 My ago	2.8 My - 160 Ky	56	96
Triassic event	ca. 200 My ago	8.3 My - 600 Ky	47	80
Cretaceous (K-T) event	ca. 65 My ago	2.5 My - 1 y	40	76

References:

Barnosky et al. (2001) Has the Earth's sixth mass extinction already arrived? *Nature* 471: 51-57.

Berner D & W Salzburger (2015) The genomics of organismal diversification illuminated by adaptive radiations. *Trends in Genetics* 31: 491-499.

Ridley M (2004) *Evolution*. Blackwell.

Schluter D (2000) *The ecology of adaptive radiation*. Oxford University Press.