Speciation

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Speciation is the evolutionary process by which novel species originate from earlier ones. This process is, in principle, equivalent to the divergence of lineages — also called **DIVERSIFICATION** — at the level of populations, but implies that new species have arisen from it. Speciation is responsible for the evolution of the organismal diversity of life on Earth.

Species concepts

There is no consensus in biology what precisely a species is. In practical terms, individuals are grouped into species in order to categorize organisms and to give these categories names, which in turn facilitates the identification of biological **SPECIMENS**. Species descriptions are usually done by taxonomists, who classify species on the basis of shared morphological characters following taxonomy guidelines. Such *diagnostic* characters are then used to distinguish between members of different species and to identify organisms, for example using field guides or identification keys. Species identification can be cumbersome because of natural variation: Individuals within a species are variable and there is usually no "ideal" or "typical" individual. Evolutionary biologists, on the other hand, interpret species as independent evolutionary units. Accordingly, members of the same species share a **GENE POOL** and fundamental evolutionary processes such as selection and **DRIFT** operate within a species.

A number of formal definitions of the category species, so called *species concepts*, have been proposed (see **Table 1** for a selection). Not one of these species concepts provides a universally valid definition of the category species. This situation is referred to as the '*species problem*'.

Table 1. *Species concepts used to define the category species (modified after Coyne & Orr 2004; Zachos 2016).*

biological species concept	A species is a group of interbreeding natural populations that is reproductively isolated from other such groups (Mayr 1963).
cohesion species concept	A species is the most inclusive populations of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms (Templeton 1989).
ecological species concept	A species is a lineages (or a closely related sets of lineages), which occupies an adaptive zone minimally different from that of any other lineage in range and which evolve separately from all lineages outside its range (Van Valen 1976).
evolutionary species concept	A species is a single lineage of ancestral-descendant lineages that evolve separately from other such lineages and have their own evolutionary tendencies and historical fate (Simpson 1961; Wiley 1978).
phylogenetic species concepts	A species is the smallest monophyletic group of common ancestry (de Querioz & Donoghue 1988). A phylogenetic species is a basal cluster of organisms that is diagnosably distinct from other such clusters (Cracraft 1989)

The *biological species concept* (BSC) is the most widely accepted and applied species definition in biology. According to the BSC, a species includes all those individuals that actually or potentially produce fertile offspring; species are separated from other species on the basis of some sort of *reproductive isolation* mechanism (see below). The BSC places the category species within the framework of population genetics and explains why members of the same species resemble each other morphologically (because they share a *gene pool*), but differ from members of other species. The BSC works well in sexually reproducing multicellular organisms, but fails in asexual organisms (**CLONES**) or in organisms with partially uniparental reproduction. Furthermore, the BSC deals badly with low

DIVERSIFICATION
The accumulation of (genetic) differences between two ore more taxa through time.

SPECIMEN
An individual organism used for scientific study or display.

GENE POOL
Total number of genes in an interbreeding population at a given time (and across all individuals).

(GENETIC) DRIFT
Random changes in allele frequencies in a population.

CLONES
Genetically identical individuals derived from the same ancestor. Clones are the result of asexual reproduction, which is found in bacteria and viruses, but also in some metazoans such as aphids, cladocerans and rotifers.

levels of **GENE FLOW** between species or with **RING SPECIES** (FIGURE 1A). Other species concepts overcome some of these issues, yet have their own drawbacks. The cohesion species concept, for example, which defines species on the basis of phenotypic cohesion through genetic and/or demographic exchangeability, applies to asexual organisms and deals with low levels of gene flow; however, the term 'phenotypic cohesion' is only vaguely defined. The ecological species concept and the evolutionary species concept are similarly vague, rendering their usage impracticable. Phylogenetic species concepts deal badly with **PARAPHYLETIC SPECIES** (FIGURE 1B) — a situation that appears to be common in nature.

GENE FLOW
The movement or exchange of genes into or through a population by interbreeding or by migration and subsequent interbreeding.

RING SPECIES
Two reproductively isolated populations are connected by a geographic ring of populations that interbreed. No morphological character can be used, except arbitrarily, to divide the ring into discrete species. A division would be meaningless, as there really is a continuum.

PARAPHYLETIC SPECIES
A species that includes most but not all descendant populations of a common ancestor. This situation can occur when one population diversifies into a new species.

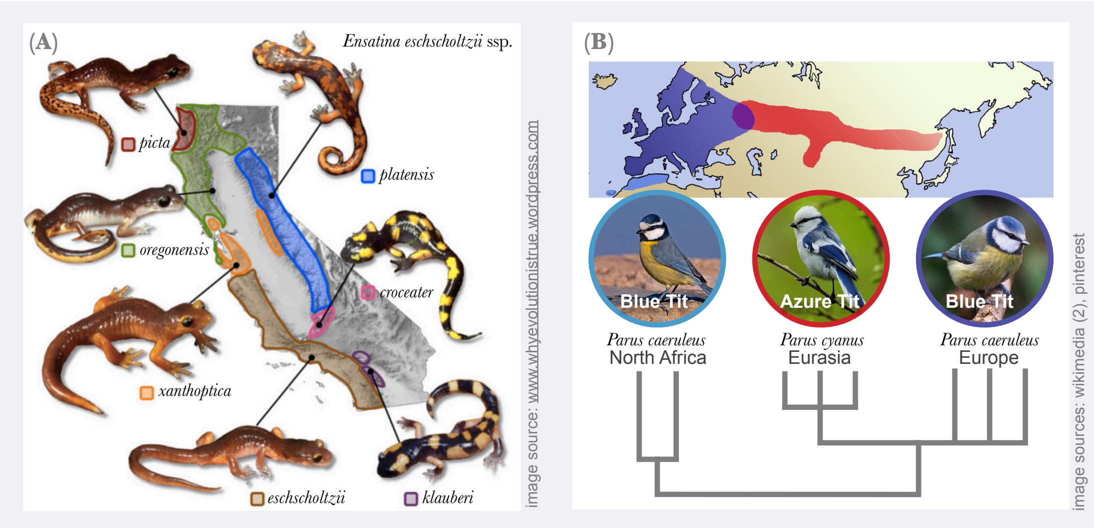

FIGURE 1. *Problems with defining species. (A) Ring species containing various subspecies of the salamander Ensatina eschscholtzii in western USA (from: Stebbins 1994). (B) The blue tit (Parus caeruleus) is a paraphyletic species. The North African subspecies P. c. degener and P. c. ultramarinus are the sister group to the European Blue Tit (P. c. caeruleus) plus the Eurasian Azure Tit (P. cyanus) (from: Salzburger et al. 2002).*

Reproductive isolation

The origin of species is a continuous process, during which an ancestral species gives rise to one or more novel species. The process is completed with the establishment of *reproductive isolation* (FIGURE 2), that is, the members of the new species do not, or cannot, interbreed anymore with members of the ancestral species. Any mechanism that prevents gene flow between (newly emerging) species is called *isolating mechanism* or *isolating barrier*.

Isolating barriers are grouped, according to when they operate during a reproductive cycle, into *premating*, *postmating prezygotic* and *postzygotic isolating barriers* (BOX 1). Premating isolation mechanisms are

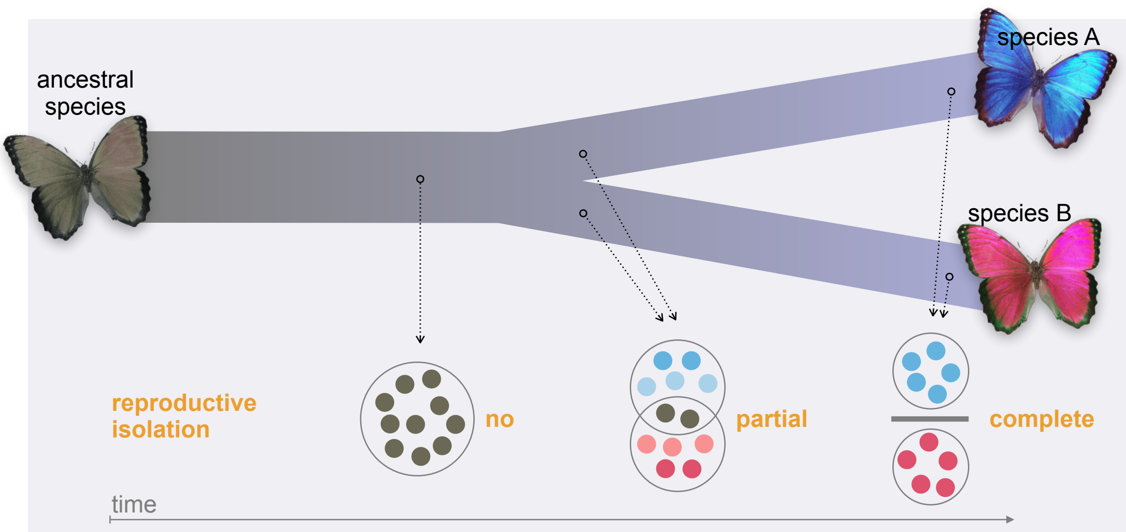

FIGURE 2. *The "speciation continuum". A speciation event is completed once reproductive isolation is fully established. In this example, two species (A and B) emerged out of the ancestral species; it is also called speciation, if the ancestral species continues to exist and only one species emerged (in this case, either A or B would resemble the ancestral species).*

Box 1: Isolating barriers (according to Coyne & Orr 2004).

Premating isolating barriers prevent the formation of a hybrid zygote by impeding gene flow *before* the transfer of sperm or pollen:

Behavioral isolation	Mutual attraction between the sexes of different species is weak or absent, preventing them from initiating courtship or copulation.
Ecological isolation	**Habitat isolation**. The adaptation to different habitats in the same general area prevents or limits gene exchange. **Temporal isolation**. Gene flow between two taxa is impeded because of different breeding/flowering times. **Pollinator isolation**. Gene flow between angiosperm species is reduced by differential interactions with pollinators.
Mechanical isolation	Copulation or pollination between two species is inhibited due to incompatibilities of reproductive structures.
Mating system isolation	The evolution of partial or complete self-fertilization or asexual reproduction prevents gene flow with members of the ancestral population.

Postmating, prezygotic isolating barriers prevent the formation of hybrid zygotes after sperm or pollen transfer but before fertilization:

Copulatory behavioral isolation	The behavior of an individual during copulation is insufficient to allow normal fertilization.
Gametic isolation	**Noncompetitive gametic isolation.** Intrinsic problems with transfer, storage, or fertilization of heterospecific gametes in single fertilizations between members of different species. **Competitive gametic isolation.** Heterospecific gametes are not properly transferred, stored, or used in fertilization when competing with conspecific gametes ("conspecific sperm or pollen preference").

Postzygotic isolating barriers reduce the viability or fertility of hybrid zygotes:

extrinsic	**Ecological inviability.** Hybrids develop normally but suffer lower viability because they cannot find an appropriate ecological niche. **Behavioral sterility.** Hybrids have normal gametogenesis but are less fertile than parental species because they cannot obtain mates.
intrinsic	**Hybrid inviability.** Hybrids suffer developmental difficulties causing full or partial lethality. **Hybrid sterility.** Hybrids suffer problems in the development of the reproductive system or gametes or suffer neurological or physiological lesions that render them incapable of successful courtship.

the most 'inexpensive', as there is no further investment into mating or reproduction. In cases where hybrids feature a reduced fitness compared to pure-bread individuals, natural selection may act to reinforce reproductive isolation due to the high costs of mating with a partner belonging to the "wrong" species. The evolution of divergent mate preferences in response to selection against hybrids is called *reinforcement*.

The origin of species

More than 150 years after the publication of Charles Darwin's seminal book "*On the Origin of Species*", the questions of how and why isolating barriers and, consequently, new species emerge remain challenging. Different modes and mechanisms of speciation have been identified.

As initially proposed by Darwin, **natural selection** plays a key role in speciation. **NATURAL SELECTION** is generally recognized as central mechanism of evolutionary change within natural populations; if selection is divergent — for example between habitats — two populations might be driven apart and new species may form. The evolution of reproductive isolation between populations by adaptation to different environments or ecological niches is called *ecological speciation.* Ecological speciation can occur in a variety of settings, including in allopatry, parapatry and sympatry (see below for details). **SEXUAL SELECTION** can also lead to, or at least contribute to, speciation. Sexual selection is one of the most potent forces mediating (premating) reproductive isolation; traits involved in mate choice, courtship and mating evolve faster than most other traits (see **TABLE 2** for some fundamental differences between natural and sexual selection).

TABLE 3. *Fundamental differences between sexual and natural selection.*

	selection based upon	competitors
sexual selection	individual fitness	other members of the same sex
natural selection	fitness of the genotype	other individuals (within the same population)

A classical distinction relates to the different **geographic conditions** under which speciation may occur (**TABLE 3**): A new species may arise in complete geographic — and, hence, genetic — isolation from its ancestor (*allopatric speciation*), it may form in a geographically contiguous setting (*parapatric speciation*), or it may emerge within the geographic range of its ancestor *(sympatric speciation*). Historically, allopatric speciation (including its variants such as *peripatric speciation*) has been considered the default mode by which new species evolve. In allopatric speciation, reproductive isolation emerges as byproduct of independent evolution in geographically isolated populations. This may occur via drift, the accumulation of different **MUTATIONS**, or **ADAPTATION** to different environments. The analysis of **GENOME** wide data, on the other hand, suggests that the exchange of genetic material (gene flow) is rather common between diversifying populations. Parapatric speciation — either along environmental gradients (*clines*) or according to *stepping stone models* — may thus be way more common than previously thought. The frequency of occurrence of sympatric speciation is controversially discussed, not least because — in many putative cases — alternative scenarios cannot be ruled out; however, mathematical models and computer simulations as well as empirical evidence (*e.g.*, from cichlid fishes in small crater lakes and palm trees on oceanic islands) suggest that it is common, too. The geographic modes of speciation (allopatric, parapatric and sympatric) provide little information about the actual mechanisms involved in the process.

TABLE 2. *Geographic modes of speciation.*

allopatric speciation	The origin of new species from geographically isolated populations; there is no gene exchange between the diverging populations *(from Greek 'allos' = different, Latin 'patria' = homeland).*
peripatric speciation	The origin of new species from a peripherally isolated population (hence, a species case of allopatric speciation); there is no gene exchange between the diverging populations *(from Greek 'peri' = adjacent, Latin 'patria' = homeland).*
parapatric speciation	The origin of new species from geographically adjacent populations; gene flow between diverging populations is neither zero nor the maximum possible *(from Greek 'para' = alongside, Latin 'patria' = homeland).*
sympatric speciation	The origin of new species without geographic isolation; gene flow between diverging populations can be zero bus is usually neither zero nor the maximum possible*(from Greek 'syn' = together, Latin 'patria' = homeland).*

MUTATION
Any change in the nucleotide sequence of an organism (compared to the parental generation), either in the form of a point mutation, a deletion/insertion, or a chromosomal rearrangement.

ADAPTATION
A feature of an organism that evolved because it improves the survival and reproductive performance of the organism. Adaptation may also refer to the process that produces such a feature.

GENOME
The entire genetic material of an organism.

NATURAL SELECTION
The process by which the forms of organisms in a population that are best adapted increase in frequency relative to the less well-adapted forms over a number of generations.

SEXUAL SELECTION
The selection on mating behavior, either through competition among members of one sex (usually males) for access to members of the other sex or through choice by members of one sex (usually females) for certain members of the other sex.

New species may also originate via **polyploidization** or as a consequence of **hybridization**. **POLYPLOIDS** arise naturally, for example because of errors during meiosis (*autopolyploidy*) or after **HYBRIDIZATION** events (*allopoyploidy*). The most common form of polyploidy in nature is tetraploidy. Tetraploids are interfertile among themselves, but reproductively isolated from the parental species (due to their different chromosomal arrangement). Hybrid speciation can occur when hybrids have a fitness advantage, for example under certain environmental conditions. Polyploid and hybrid speciation are common in plants, but are also known from animals.

POLYPLOIDS
Organisms that contain more than two homologous sets of chromosomes such as triploids or tetraploids.

HYBRIDIZATION
Crossbreeding between members of two distinct taxa (*e.g.*, populations, species, genera)

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