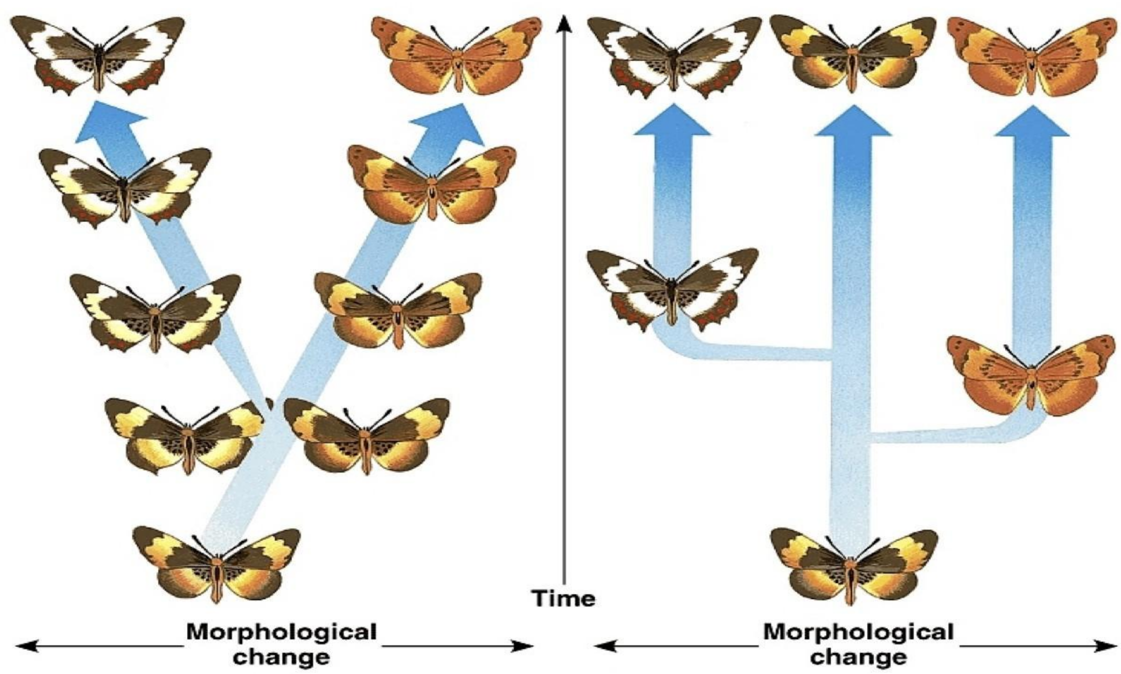
Punctuated equilibrium & Stasis

Punctuated equilibrium (also called **punctuated equilibria**) is a theory in evolutionary biology which proposes that once a species appears in the fossil record the population will become stable, showing little evolutionary change for most of its geological history. This state of little or no morphological change is called *stasis*. When significant evolutionary change occurs, the theory proposes that it is generally restricted to rare and geologically rapid events of branching speciation called cladogenesis. Cladogenesis is the process by which a species splits into two distinct species, rather than one species gradually transforming into another.

Punctuated equilibrium is commonly contrasted against phyletic gradualism, the idea that evolution generally occurs uniformly and by the steady and gradual transformation of whole lineages (called anagenesis). In this view, evolution is seen as generally smooth and continuous.

In 1972, paleontologists Niles Eldredge and Stephen Jay Gould published a landmark paper developing their theory and called it *punctuated equilibria*. Their paper built upon Ernst Mayr's model of geographic speciation, I. Michael Lerner's theories of developmental and genetic homeostasis, and their own empirical research. Eldredge and Gould proposed that the degree of gradualism commonly attributed to Charles Darwin is virtually nonexistent in the fossil record, and that stasis dominates the history of most fossil species.



(a) Gradualism model (b) Punctuated equilibrium model

The concept of **punctuated equilibria** was developed to explain a pervasive and intriguing evolutionary pattern: most species change little if at all after they first appear in the fossil record. In many cases, individual species lineages persist for millions of years without showing any significant morphological change. The idea was described in detail in Eldredge and Gould (1972), where the term was coined, although important aspects of the idea were first developed in Eldredge (1971). Punctuated equilibria actually comprises several different and related observations. These include:

1. the fossil record contains a rich source of data useful for developing important evolutionary hypotheses;
2. speciation typically happens allopatrically, in narrow and geographically restricted populations containing relatively few individuals;
3. species are not slowly and gradually adapting and evolving over long stretches of geological time;
4. species lineages that show stasis – or an absence of morphological change – dominate the fossil record and provide useful information about the tempo and mode of evolution;
5. the first appearance of a new species in the fossil record usually does not represent its point of evolutionary origin but rather the migration of a new geographically isolated species back into its ancestral range, with concomitant expansion in abundance; and
6. speciation typically takes on the order of 5,000 to 50,000 years to occur – far shorter than the average duration of species in the fossil record.

Punctuated equilibria's significance extended beyond explaining patterns of within species evolution. It opened up several new avenues of research and helped spawn a new discipline: macroevolution; it further led to a greater appreciation of the hierarchical structure of nature and its implications for understanding evolutionary patterns and processes. Finally, it helped re-integrate paleontology with the mainstream of evolutionary biology.

Mechanisms of stasis

One of the interesting research areas that punctuated equilibria spawned was the search for mechanisms that might cause stasis. Part and parcel with this issue was the puzzling fact that over historical time scales – decades to centuries – species were capable of showing large amounts of change, yet over millions of years they were basically static (Eldredge et al 2005). A variety of mechanisms for stasis have been proposed and discussed (e.g. Eldredge and Gould 1972; Stanley 1979; Eldredge 1985a; Lieberman et al. 1995; Lieberman and Dudgeon 1996; Sheldon 1996; Gould 2002; Eldredge et al 2005). One idea first suggested by Eldredge and Gould (1972) was that organisms within species might possess certain developmental constraints that act to canalize and restrict the amount and type of morphological change that can occur. This mechanisms is still thought to play some role, but it has not been fully endorsed because it seems that organismal development might not be all that canalized (Gould 2002; Eldredge et al 2005): consider the tremendous range of body type differences that have been produced relatively recently in domestic dog breeds.

Another mechanism that has been proposed is based on the fact that species are usually broken up into different geographic populations (Eldredge 1989; Lieberman et al 1995; Lieberman and Dudgeon 1996; Eldredge et al 2005). Each one of these may undergo a quasi-independent adaptive history. Morphological changes will occur in different populations and the total change within a species through time equals the net sum of the changes in all of its component populations. Given that each of these populations will be adapting to different environmental parameters, morphological change will usually be in different directions of morphospace. Therefore, the sum total of the changes will typically cancel out (Fig. 5). Furthermore, as long as different populations can still interbreed, changes will tend to be homogenized and the net result will be stasis.