

Punctuated equilibrium (or **punctuated equilibria**) is a theory in [evolutionary biology](#) which states that most [sexually reproducing](#) species will show little to no evolutionary change throughout their history. When evolution occurs it happens sporadically (by [splitting](#)) and occurs relatively quickly compared to the [species'](#) full duration on [earth](#). Punctuated equilibrium is commonly contrasted against the theory of [phyletic gradualism](#), which hypothesizes that most evolution occurs uniformly and by the steady gradual transformation of whole lineages ([anagenesis](#)). Punctuated equilibrium is the currently favored theory for the fluctuating patterns of evolution observed in the [fossil record](#).

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Punctuated Equilibrium's History

Punctuated equilibrium originated as an extension of [Ernst Mayr's](#) concept of genetic revolutions by [peripatric](#) and [allopatric](#) speciation. Although the workings of the theory were proposed and specifically identified by Mayr in [1954](#), most [historians of science](#) recognize [Niles Eldredge](#) and [Stephen Jay Gould's 1972](#) paper as the principal source of its acceptance (by both [paleontologists](#) and [evolutionists](#)) and as the foundational document of a new and serious paleontological research program ([Mayr](#) 1992: 25-26, [Shermer](#) 2001: 102-113). Punctuated equilibrium differed from Mayr simply in that [Eldredge](#) and [Gould](#) had placed considerably greater emphasis on stasis, whereas Mayr was generally concerned with explaining the morphological discontinuity (or punctuational patterns) found in the fossil record.

The Eldredge and Gould paper^[1] was presented at the [Annual Meeting of the Geological Society of America](#) in [1971](#). The symposium focused its attention on how modern [microevolutionary](#) studies could revitalize various aspects of paleontology and macroevolution. Tom Schopf, who organized that year's meeting, assigned Stephen Jay Gould the topic of speciation. Gould recalls that:

"Eldredge's [1971](#) publication [on [Paleozoic trilobites](#)] had presented the only new and interesting ideas on the paleontological implications of the subject—so I asked Schopf if we could present the paper jointly." (Gould [2002](#): 775)

They did. According to Gould:

"the ideas came mostly from Niles, with yours truly acting as a sounding board and eventual scribe. I coined the term *punctuated equilibrium* and wrote most of our [1972](#) paper, but Niles is the proper first author in our pairing of Eldredge and Gould." (Gould [1991](#))

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Tempo and Mode

Ernst Mayr's paper "[Change of genetic environment and evolution](#)" ([1954](#)) emphasized the homogenizing effects of [gene flow](#) and the stabilizing influence of large interbreeding populations. These populations exemplified "ecotypic variation." Peripherally isolated populations, in contrast, possess "typostrophic variation" which "have the characteristic features of incipient species, but what is more important they often are species or incipient species of an entirely new type. That is, they may have morphological or ecological features that deviate quite strikingly and unexpectedly from the parental 'pattern' " ([1954](#):160)

Stephen Jay Gould summarized the theory, and its consequences for punctuated equilibrium, in a [1977](#) essay for [Natural History](#):

"A new species can arise when a small segment of the ancestral population is isolated at the periphery of the ancestral range. Large, stable central populations exert a strong homogenizing influence. New and favorable mutations are diluted by the sheer bulk of the population through which they must spread. They may build slowly in frequency, but changing environments usually cancel their selective value long before they reach fixation. Thus, phyletic transformation in large populations should be very rare—as the fossil record proclaims. But small, peripherally isolated groups are cut off from their parental stock. They live as tiny populations in geographic corners of the ancestral range. Selective pressures are usually intense because peripheries mark the edge of ecological tolerance for ancestral forms. Favorable variations spread quickly. Small peripheral isolates are a laboratory of evolutionary change.

"What should the fossil record include if most evolution occurs by speciation in peripheral isolates? Species should be static through their range because our fossils are the remains of large central populations. In any local area inhabited by ancestors, a descendant species should appear suddenly by migration from the peripheral region in which it evolved. In the peripheral region itself, we might find direct evidence of speciation, but such good fortune would be rare indeed because the event occurs so rapidly in such a small population. **Thus, the fossil**

record is a faithful rendering of what evolutionary theory predicts, not a pitiful vestige of a once bountiful tale." (1980:184)

In the late 19th century, following [Charles Darwin](#)'s publication of *The Origin of Species*, Moritz Wagner had similarly proposed that isolation is actually necessary for speciation.

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Misconceptions

Punctuated equilibrium is often confused with [quantum evolution](#), [saltationism](#), [catastrophism](#), and with the phenomenon of [mass extinction](#), and is therefore mistakenly thought to *oppose* the concept of [gradualism](#). It is actually more appropriately understood as a *form* of gradualism (in the strict and literal sense of biological continuity). This is because even though the changes are considered to be occurring relatively quickly (relative to the species geological existence), changes are still occurring incrementally, with no great changes from one generation to the next. This can be understood by considering an example: Suppose the average length of a limb on a particular species grows 50 centimeters (20 inches, a large amount) over 70,000 years (a geologically short period of time). If the average generation is seven years, then the given time span corresponds to 10,000 generations. Thus, on average, the limb grows at the minute, gradual rate of only 0.005 cm per generation (= 50 cm/10,000 generations).

Punctuated Equilibrium is frequently contrasted with [phyletic gradualism](#), though critics, notably [Richard Dawkins](#), have argued that phyletic gradualism is merely a [straw man](#). Eldredge and Gould's advocacy of the theory brought punctuated equilibrium much attention, especially since they phrased it in terms that made it appear to be a radical re-thinking of evolutionary theory. **The resulting debate stirred up in evolutionary circles was misrepresented by some creationists to portray Darwinism as a "theory in crisis."** Some detractors among evolutionary biologists wryly termed punctuated equilibrium "evolution by jerks." (It is now sometimes referred to by the slang "punk eek," with no negative connotations implied.) The actual differences between the various evolution theorists were not as large as they were made to appear. Gould himself later said that the theory did not in fact refute Darwin's gradualism, but just added the ideas of catastrophism and stasis.

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Relation to Darwinism

The sudden appearance and lack of substantial gradual change of most species in the geologic record—from their initial appearance until their extinction—has long been noted, including by Charles Darwin ([1859:301](#), [1871:119-120](#)) who appealed to the imperfection of the record as the favored explanation. Nevertheless, with the influence of catastrophism, Darwin needed to forcefully stress the gradual nature of evolution. It is

often incorrectly assumed that he insisted that the rate of change must be constant, or nearly so. Though in *The Origin of Species* Darwin wrote that "the periods during which species have undergone modification, though long as measured in years, have probably been short in comparison with the periods during which they retain the same form." (1872:619) Thus punctuationism in general is consistent with Darwin's conception of evolution, and with the independent proposals of [natural selection](#) by [William Charles Wells](#), [Patrick Matthew](#), [Charles Darwin](#) and [Alfred Russel Wallace](#).

According to the theory of punctuated equilibrium, "peripheral isolates" are considered to be of critical importance for speciation. However, Darwin wrote, "*I can by no means agree...that immigration and isolation are necessary elements. . . . Although isolation is of great importance in the production of new species, on the whole I am inclined to believe that largeness of area is still more important, especially for the production of species which shall prove capable of enduring for a long period, and of spreading widely.*" (1859:105-106)

Darwin explained the reasons for this belief as follows:

"Throughout a great and open area, not only will there be a greater chance of favourable variations, arising from the large number of individuals of the same species there supported, but the conditions of life are much more complex from the large number of already existing species; and if some of these species become modified and improved, others will have to be improved in a corresponding degree, or they will be exterminated. Each new form, also, as soon as it has been improved, will be able to spread over the open and continuous area, and will thus come into competition with many other forms ... the new forms produced on large areas, which have already been victorious over many competitors, will be those that will spread most widely, and will give rise to the greatest number of new varieties and species. They will thus play a more important role in the changing history of the organic world." (1859:107-108)

Thus punctuated equilibrium contradicts some of Darwin's ideas regarding evolution, but accords with others.