Punctuated Equilibrium

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All evolution, of course, must be gradual, in that each generation must not be too unlike the previous generation, or mating would be impossible. Punctuated equilibrium is not saltationism, a defunct theory that states that speciations occur in single large steps. Rather, punctuated equilibrium states that populations remain stable for long periods of time, evolving little or not at all; these periods of time are called *stases*. In the most common occurrence of speciation, according to punctuated equilibrium, small, isolated populations evolve rapidly, so that speciation takes place over about ten thousand to a million years. This period of time is a geological instant, but it still allows plenty of time for gradual change at a fast rate to produce a new species.

Punctuated equilibrium explains how large, stable populations can produce new species: the large population itself doesn't change, but small isolated "pocket" populations might, resulting in branching rather than linear species histories. It also explains the relative scarcity of transitional forms, particularly between species (rather than between larger groups), in the fossil record. If transitional forms only exist for a few thousand years, often in a small geographical location different from its later range, then the odds are against fossils being formed, found, and described.

Mechanism

Speciation under punctuated equilibrium is usually a special case of allopatric speciation, in which the speciation events take place in isolation from the parent species (Ridley 1993, 511). The theory of punctuated equilibrium contends that the isolated sub-population must be small, and that the speciation event takes place over periods of as little as "five to fifty thousand years" (Eldredge 1995, 98) or as much as "hundreds of thousands to millions of years" (Gould 1995, 137); regardless, the period is almost negligible in terms of geologic time. Between speciation events are long periods of "stasis," during which species evolve very little or not at all.

Punctuated equilibrium should not be confused with saltationism, a theory in which a new species may arise in single generation through a macromutation. Saltationism rejects Darwin's model of gradual change through generations. Dawkins (1986, 231-235) presents several statistical arguments against saltations being a significant force in evolution. The simplest of these arguments concerns the individual who differs enough from its parents to be considered a member of a new species (i.e. who cannot breed with its parental species); such an individual would die out, unable to breed and propagate its lineage.

Rather than being a saltationist theory, punctuated equilibrium is a modification of Darwin's gradualist model; essentially it is a theory of differential rates of evolution, carried to an extreme degree. A theory providing a mechanism for punctuated equilibrium requires explanations for both stasis and the punctuations during which evolution proceeds rapidly.

Stable conditions will, of course, lead to stable adaptation, i.e. no evolutionary change, and can account for stasis. But punctuated equilibrium proposes that species remain in stasis nearly all of the time, even when the environment is changing. Eldredge (1995, 78-79) attributes this phenomenon to "habitat tracking," in which species migrate to follow the habitat they are adapted for, rather than "adaptation tracking," in which the species adapts to the new habitat through natural selection. As Eldredge contends, "As long as a suitable habitat can be found, a species will move rather than stay put and adapt to new environmental regimes." Since the conditions (if not the location) of the habitat remain fairly constant, stabilizing selection causes stasis. Eldredge even cites a study of brachiopods which suggests that habitat tracking is more conducive to stasis than stable conditions, which demonstrate gradual change (1995, 80-81).

To aid as an illustration to the model, Eldredge and Gould constructed a contrasting model whose extreme form they called phyletic gradualism. Under phyletic gradualism, the rate of evolution is assumed to be fairly slow and constant, and speciation events occur through transformation of a single lineage with a large population over time (Ridley 1993, 511-512). Because the population is so large, new species do not branch from the parent species; interbreeding with other members of the population would swamp them before they could become reproductively isolated. Instead, the population as a whole would vary (Dawkins 1986, 237).

Punctuated equilibrium, on the other hand, proposes that speciation occurs as a splitting of lineages. Reproductive isolation begins with physical isolation of a small sub-population, and the small size of the isolated population renders it relatively unstable evolutionarially. The conditions that allow stasis to occur are reversed, and evolution in the isolated population occurs at a very fast rate until the conditions for stasis are met again.

Species sorting and the role of extinction

Because under punctuated equilibrium new species are formed via branching events rather than "replacements" (i.e. situations wherein one species transforms into another), the total number of species is increasing. Extinction culls those species, so that the total number of species extant at any given time is only a fraction of the total number of species which existed before that time. According to Raup (1991, 3-4), 99.9% of all species which have ever existed are now extinct. Both Gould (1989) and Raup (1991) conclude that extinctions, especially mass extinctions, are due more to uncontrollable environmental circumstances which affect species than to the species' own fitness or adaptability.

Eldredge (1995) defines "species sorting" (also called "species selection) as "differential speciation or extinction of species within a larger group"; he clarifies that "Some lineages speciate at a higher rate than others, and some species are more prone to extinction than others" (119). These varying rates of speciation and extinction, according to Eldredge, produce definite patterns in the fossil record.

Eldredge emphasizes that species sorting is not meant to replace natural selection in the formation of anatomical or behavioral adaptations of species; rather, it acts as "a major determinant of the fate of adaptations in evolutionary time" (1995, 120). Species sorting determines which adaptations survive, not which adaptations form, or how they form.

Dawkins cites a concept which he says Eldredge and Gould call "Wright's Rule." Wright's Rule says that new species do not inherently tend toward any particular direction; for example, it "suggests that there is no systematic tendency for newly branched-off species to be larger than their parent species" (1982, 104-105). Wright's Rule coupled with evolution operating according to the tenets of punctuated equilibrium results in species selection. If a lineage tends to produce species with larger and larger individuals, the cause is due to the species with smaller individuals becoming extinct, not to species with smaller individuals failing to arise.

Dawkins doubts that Wright's Rule applies in all cases, since often the adaptations of new species involve more than a single characteristic. If a new species' adaptations include a dozen new characteristics, then chances are that these characteristics are related to one another, rather than being random as predicted by Wright's Rule (1982, 106). Thus even accepting punctuated equilibrium, Dawkins doubts that species selection occurs, at least in some situations.

Testing the theory

Punctuated equilibrium predicts that the fossil record will display long gaps during which species change little or not at all, and that is exactly what the fossils do show (Ridley 1993, 513). But an explanation was already in place for this apparent pattern of punctuated evolution: the incompleteness in the fossil record, which

Darwin (1964, 287-290) discussed in detail. Therefore the observed rareness of transitional fossils is no kind of special evidence for the theory.

The fossil record can't provide much evidence from the brief periods of speciation, but paleontologists can turn to the long periods of stasis to find support for the theory. Gould (1995, 141) emphasizes the need for solid evidence to support the theory, explaining that "Some people have a false impression that claims for stasis rely on negative evidence, or absence of demonstrated changes. On the contrary, stasis should be a positive conclusion based upon hard anatomical evidence of non-change through substantial time." Ridley (1993, 513) stresses that since paleontologists must include a range of forms within each species they define, the anatomical evidence for stasis must be biometric and be sampled from a broad range of strata to show that gradual change is not taking place and rather that stasis is in effect.

Is punctuated equilibrium a "new" theory?

Dawkins (1986, 240-252) argues that punctuated equilibrium is not a "new" theory. Evolution under punctuated equilibrium occurs gradually, as it was assumed to do under Darwinism before punctuated equilibrium was proposed. Dawkins notes that Eldredge and Gould are "truly as gradualist as anybody else" (1986, 243; see also Eldredge [1995, 98-100]). Their theory merely proposes that the rate of evolution varies. According to Dawkins, this conclusion arises out of common sense; no biologist ever claimed that the speed of evolution has never varied. Dawkins says that "It isn't true that Darwin believed evolution proceeded at a constant rate" (243), and implies that neither has any serious evolutionist since his time.

Therefore, concludes Dawkins, punctuated equilibrium is in no way a "new" theory. He paints a picture of Eldredge and Gould as attempting to sell their theory as radically new material opposed to traditional "gradualist" Darwinism when in fact they are merely restating old news. Darwin (1964) says about gradualism:

> "Nothing can be effected, unless favourable variations occur, and variation itself is apparently always a very slow process. The process will often be greatly retarded by free intercrossing. Many will exclaim that these several causes are amply sufficient to stop the action of natural selection. I do not believe so. On the other hand, I do believe that natural selection will always act very slowly, often only at long intervals of time, and generally on only a very few of the inhabitants of the same region at the same time. I further believe that this very slow, intermittent action of natural selection accords perfectly well with what geology tells us of the rate and manner at which the inhabitants of this world have changed." (108-109)

In the fourth and following editions of On the Origin of Species, Darwin added that the rate of evolution may change, implying that what is now called "stasis" is possible (cited by Dawkins [1986, 244]). (Eldredge [1995] himself says that the concept of differential rates of evolution existed even before Darwin.) Darwin also recognized that it often operates on subpopulations of individuals. He did not, however, see an active mechanism for stasis, since he wrote that he didn't believe that any of the causes he recognized would be enough to stop natural selection. Instead he implied that stasis is merely a passive occurrence, that natural selection merely "stops" (rather than having its effects blocked by an active mechanism).

For punctuated equilibrium to be a "new" or revolutionary theory, it must propose something which Darwin did not recognize as at least possible. Punctuated equilibrium only fulfills this condition if it includes an active mechanism for stasis, a mechanism by which a species can experience selection pressure and small enough population size to overcome "inertial" resistance, and still not evolve. If no active mechanism is proposed, then Eldredge and Gould's "theory" is nothing more than a selective restatement of Darwin's own proposals.

Dawkins plays down the importance of the key element of punctuated equilibrium: the great emphasis placed upon stasis as the normal condition of populations. Though he recognizes that "It is the emphasis on stasis that is the punctuationists' real contribution" (1986, 243) he denigrates the importance of this contribution.

Dawkins offers a mechanism of "buffered gene pools," originally conceived by Sewall Wright and Ernst Mayr and later by Maynard Smith, as an active mechanism for stasis, derived from a non-paleontological viewpoint (1982, 102-103). Yet in Dawkins (1986), he implies that this mechanism, "the idea that groups of genes are so well adapted to each other that they resist invasion by new mutant genes which are not members of the club" (1986, 247), was proposed by "punctuationists" (suggesting Eldredge and Gould), who themselves approach evolutionary theory from a very paleontological perspective (described by Eldredge (1995) as "naturalist"). He then dismisses the mechanism of buffered gene pools as an active stabilizing factor leading to stasis because under artificial selection, it imposes no restraint; breeders selecting for a particular trait encounter no resistance due to the balance of genes adapted for each other being upset, so neither should natural selection, according to Dawkins (1986, 247).

Under such a scheme, it appears that the Eldredge and Gould blundered when they suggested that stasis arises via an active resistance to evolutionary change. But Eldredge (1995, 78) cites a completely different mechanism from the one Dawkins claims for them in Dawkins (1986): habitat tracking. Via this mechanism, a species will tend migrate rather than evolve when faced with selection pressure; thus very little or no adaptive change need take place. Stasis is granted an active mechanism, but it isn't the one Dawkins (1986) claims it to be. Why Dawkins (1982) attributes the buffered gene pool mechanism to non-paleontologists Wright and Mayr and later Smith, while Dawkins (1986) attributes it to "punctuationists," is unclear.

With this active mechanism of "habitat tracking," punctuated equilibrium becomes a real, rather than perceived, contribution to evolutionary theory. The study of punctuated equilibrium as a new modification of Darwinism is validated.

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[1] This paper was written in December 1997. It explains the basics of the model of Darwinism known as "punctuated equilibrium," including its mechanisms, the role of extinction in it, and the proper ways to test it. It also considers the question raised by Richard Dawkins regarding its real theoretical value: is it really a new and revolutionary theory, or is it just another modification of Darwinism?