Punctuated equilibrium: a possible alternative to phyletic gradualism research pa...

Science, Genetics

Abstract

Theory of evolution as proposed by Darwin has for long hinged on the fossil records to prove the process of evolution. However, the prevalent gaps in the fossils led way to the development of the punctuated equilibrium theory that was proposed by Eldredge and Gould as an alternative to Darwin's phyletic gradualism theory. The punctuated equilibrium postulated that speciation occurs in an isolated peripheral subsect of population as a rapid change after a period of stasis. Unlike the anagenetic speciation of phyletic gradualism, punctuated equilibrium promotes the concept of cladogenetic speciation. However, punctuated equilibrium does consider rapid anagenetic speciation as a part of stasis. Review of literature and current studies indicate that these two modes of evolution, as different as they are in concept and manifestations, are part of the same puzzle: evolution. Computational models that take into account rate of evolution and extinction have been helping evolutionary biologists to understand which of the two modes and their manifestations conform better to the fossil records. However, the results have revealed that neither the phyletic gradualism nor the punctuated equilibrium explain all the micro-and macro-evolutionary changes in the environment; nevertheless, when these two modes are applied together to modelling techniques, some of the evolutionary mysteries make sense. Current studies summarize that phyletic evolution occurs in an environment that promotes stable and gradual growth while the occurrence of punctuated equilibrium is copious in harsh and unstable environments. This statement proves the hypothesis of this paper that

punctuated equilibrium and phyletic gradualism are complementary and not contradictory.

Punctuated equilibrium versus phyletic gradualism: Contradictory or complementary?

Punctuated equilibrium is an alternate theory of speciation that was proposed by Eldredge and Gould in 1972 to Darwin’s theory of phyletic gradualism. This paper tries to analyze whether PUNCTUATED EQUILIBRIUM AND PHYLETIC GRADUALISM ARE CONTRADICTORY OR COMPLEMENTARY. Review of past literature suggests that phyletic gradualism explains anagenesis (Saylo, Escoton and Saylo 32), especially in pelagic organisms (Hull and Norris 21224) but fails to explain cladogenesis, adaptive radiations, living fossil and generation time (Monroe and Bokma 105). Even Gould and Eldredge have referred to punctuated equilibrium as a complementary theory to phyletic gradualism in a publication made 21 years after their original paper (223) as opposed to referring it as an alternate theory as they had done earlier (82). Therefore, these literatures suggest that as different as these theories are, in combination they might be able to answer some of the evolutionary mysteries.

In evolutionary biology, fossil records are considered important clues to evolution, albeit, incomplete because these fossil records seem to have a prevailing pattern of gap between intermediary species. This caused the biologists to question if these patterns were a consequence of poor fossilization or a deliberate act of abrupt and rapid speciation. The school of thought that considered these gaps as an imperfection in an otherwise solid theory of evolution were the followers of phyletic gradualism. Darwin is considered as one of the key personalities who fueled the idea of speciation via natural selection that stemmed from the slow process of phyletic gradualism. Eldredge and Gould suggested that these gaps are not imperfections but rather a static state that led to a sudden spurt of growth and speciation before fossilization could occur (Eldredge and Gould 83).

Concepts of phyletic gradualism

Evolutionary biologists identify two mechanisms by which new species could come into existence. The first possible mechanism is gradual phyletic transition of an entire population into a new species through natural selection of traits that would aid in survival. The second mechanism proposed is speciation by splitting of a lineage (Eldredge and Gould 87). Phyletic gradualism viewed both of these mechanisms through the eyes of slow change, which brought forth the four basic concepts of this theory, namely, slow transformation from an ancestral species to the descendant species; slow and even transformation; transformation of an entire population; and occurrence of transformation over a large geographic habitat of the population. If this were true, except for soft-bodied organisms, all the hard-bodied intermediary forms must have left fossilized clues; but such evidences have not been found for any species possibly due to incomplete stratigraphic sequences (Eldredge and Gould 89).

Even though such breaks in morphological evidences in fossils is considered as imperfect record by phyletic gradualists, punctuated equilibrium considered these breaks as genuine gaps that resulted not from gradual transition but rapid cladogenesis, leaving no time for intermediaries to be fossilized. Natural selection was one of the underpinning concept for this slow transformation, according to Darwin, who hypothesized that the process of survival favored those organisms that had traits that aided in surviving their current environment. Darwin’s theory also suggested that evolution is constant and does not always aim at speciation through lineage splitting (Saylo, Escoton and Saylo 28).

Some of the innate flaws of phyletic gradualism is that it does not answer how the rapid emergence of diverse species owing to adaptive radiations and environmental changes occurs if evolution was supposed to be even and slow. It did not predict the remarkably unchanged genetic makeup of the descendant from its ancestral genes. It also does not explain the phenomenon of sudden extinction of species that had evolved gradually through natural selection, only to wither away in the next dramatic climate change. Living fossils are another perplexing product of evolution that do not show any morphological or genetic variance when compared to their fossilized ancestors; such a long stasis is clearly a deviation from the underlying concept of transformation as depicted by phyletic gradualism (Monroe and Bokma 105).

Evolutionary forms that prove the existence of gradualism

It is evident from the growth pattern of marine planktons and their fossil records that speciation has always been unidirectional, without branching. Literature suggests that phyletic gradualism is seen in cosmopolitan organisms (species that are spread worldwide in similar habitats) that have the ability to adapt quickly to their changing environment due to certain genotypes owing to a constant stream of gene flow (Hull and Norris 21224). The same can be said of evolution of humans who travelled widely and were deemed cosmopolitan with constant flow of new genes. However, the coexistence of the ancestral species with the new species even after the lineage splitting speciation could only be explained by punctuated equilibrium (Eldredge and Gould 98).

Concepts of punctuated equilibrium

Eldredge and Gould that allopatric speciation could have manifested itself upon isolated species, resulting in punctuated or pulsed morphological changes that were not experienced by the ancestral forms, leading to the ' gaps' in fossil records. Evolution was not a slow unfolding process but a spectacle that was punctuated with periods of remarkably rapid growth, possibly due to better environmental conditions and accumulation of macro-mutations (Eldredge and Gould 83).

Some of the fossil organisms that sparked this theory were Micraster sp., Liostrea sp. and Gryphae sp. Two species of Micraster were thought to have evolved from the other; it was later proved that the two species were not descendants but probably evolved in tandem and shared similarity in morphology. Similarly, the genus Gryphae was thought to be a descendant of Loistrea through phyletic gradualism; however, lack of intermediary forms led to the alternate theory (Eldredge and Gould 99).

Eldredge and Gould tried to prove their theory by studying the pulmonate snail, Poecilozonites bermudensis zonatus. Gould was able to elucidate that P. b. zonatus gave rise to four species that were geographically isolated from their ancestor. He concluded that the four species arose at different geographic locations, at different times and independently of one another from the same lineage of P. b. zonatus and not as a consecutively lineage as suggested by phyletic gradualism. Gould suggested that the speciation of the same ancestor into four species at various times could have been due to environmental factors (Eldredge and Gould 100).

Mechanics of punctuated equilibrium

One of the key differences between phyletic gradualism and punctuated equilibrium is that according to punctuated equilibrium, a population does not gradually evolve into a new species; rather an isolated part of the ancestral population undergoes rapid change as a small community. One can deconstruct punctuated equilibrium into seven distinct components, namely, stasis, isolation, species selection with rapid change, no fossilization, reunion with ancestral population, another stasis and fossilization (Saylo, Escoton and Saylo 31).

Stasis

Many hypotheses and theories have been put forth to explain the process and existence of stasis. Stabilization selection is one such theory, which suggests that stabilization selection selects stable average phenotypes over other unstable traits and expresses it over many generations. Trait plasticity is another concept that hinges on the ability of a single trait to change as per the environment, thereby conferring stability to the species. The hyperstable niche theory suggested that an organism that could adapt or mutate to a hyperstable habitat could attain longevity and remain static until it fossilized.

Organisms that adapted to an unstable niche could have become extinct leaving no fossil records. According to Eldredge and associates, the only way an organism could not be static is by developing a new genotype, which would integrate itself in a population and spread throughout the niche. Failing to achieve even one of the above would lead to stasis (Monroe and Bokma 106).

Isolation

Peripheral population are thought to be formed due to isolation from rest of the population. Such an isolation could have been a result of natural calamities, geographic topography or a response to threat. For example, in a lake community, organisms would be separated from the local population during high temperature period when the water level drops down. On the other hand, restricted gene flow due to natural selection might also cause some species to move away to new location causing isolation (Saylo, Escoton and Saylo 31).

Rapid change

Studies have revealed that natural selection within an inbreeding population could prevent gene flow, which in turn could result in speciation as a mechanism of survival within the left out individuals while permitting the ancestral population to continue through natural selection. This concept is marriage between phyletic gradualism and punctuated equilibrium. Molecular genetic studies have revealed a pattern of rapid nucleotide divergence in periods that correspond to speciation events in fossil records.

The rapid changes were also attributed to allopatry (Monroe and Bokma 107).

No fossilization

Rapidly changing organisms might not live long enough to fossilize and their adaptations are lost with them. Therefore, this could be a reason for the missing links that phyletic gradualists calls as the gap (Saylo, Escoton and Saylo 32).

Reunion with ancestral

More environmental and geographic changes could reunite the morphed species with its ancestral lineage leading to species richness (Saylo, Escoton and Saylo 31).

Second stasis

With overpopulation, natural selection, genetic homeostasis, restricted gene flow and competition, the evolution might come to a standstill, leading to extinction and fossilization. Organisms that diverge at this point through rapid change might fail to leave fossils (Saylo, Escoton and Saylo 31).

Gradualism and stasis

In current scientific setup, these two modes of trait evolution are determined using computational models with input from fossil records that are based on random walk Brownian movement through constant rate gradualism, stasis (as stasis is data, suggested by Eldredge and Gould) and direction of the clad evolution. The output have been a mix suggesting that no evolutionary process could be clearly pulsed or clearly gradual (Pennell, Harmon and

Uyeda 24). It can be inferred from this idea that speciation is rapid in the incipient stage and phases out into gradualism and reaches stasis, much like the stationary phase of a growth curve (Monroe and Bokma 107). This concept conforms to the thesis statement of this paper that these two modes of evolution are most probably complementary than contradictory.

Anagenetic and cladogenetic speciation

One of the major differences between the phyletic gradualistic mode and the punctuated equilibrium mode is the direction of evolution. While phyletic gradualism roots for anagenetic speciation, punctuated equilibrium stands by cladogenetic speciation. Paleontological data in association with earlier evolutionary modelling have made poor progress in demarcating the two types of speciation in a lineage. It has also not been possible to distinguish the contribution of anagenetic and cladogenetic speciation to the traits (Pennell et al. 26).

One approach to evaluate the impact of anagenetic and cladogenetic speciation could be to correlate the rate of speciation with evolution of the new trait attained by the new species. Such a model would provide the significance of the evolved trait but would not provide information regarding the type of speciation or account for extinction (Pennell et al. 26). Such a discrepancy has been attributed to the simplified assumptions that were used in modelling. For example, assuming that punctuated equilibrium occurs over normal distribution because phyletic gradualism does so is an assumption with no rationale (Monroe and Bokma 108).

An evolution model that could account for both gradualism and punctuated equilibrium along with extinction might produce a statistically relevant data (Monroe and Bokma 108). One such model describes that, to understand the basis of cladogenesis in punctuated equilibrium a computational and statistical model must be designed to incorporate a list of probable events that could occur within a short duration. The model, binary state speciation extinction (‘ BiSSE’) mode uses parameters such as rate of speciation within a clad, rate of trait evolution and rate of extinction and gives output that contain data on anagenesis and cladogenesis of the species (Pennell et al. 28).

Microevolution and macroevolution

Microevolution such as speciation at a clad level are too small to result in such diverse form. Moreover, if one were to consider that speciation is gradual, then it is impossible to fathom the current complex and innumerous life forms from simple unidirectional anagenetic speciation. Punctuated equilibrium forms a better hypothesis for extrapolation to macroevolution when compared to Darwin’s gradualism. A spurt in speciation could be a result of conducive environment such as lack of predators or competition in a geographic location away from the ancestral population. Rapid speciation would inevitably require adaptation to the new genotype and phenotype, failing which the newly evolved species could become extinct. In such cases, it is possible to imagine certain species flourishing well while some just fade away (Eldredge and Gould 108).

Evidences of plausible punctuated evolution

Gould and Eldredge postulated that for an evolutionary sequence to be a potential case of punctuated equilibrium (indirectly referring that there might be other possible evolutionary mechanisms) it must have the following four characteristics (224).

Cases with stasis

Punctuated equilibrium could be a possible mode of evolution is organisms that exhibit prolonged stasis. Such a stasis might as well be a phase of rapid anagenetic speciation. Therefore, it would be essential to prove that the stasis is part of a cladogenetic speciation and the existence of a putative ancestor lineage that gave rise to multiple branches of the species. Studies have documented such organisms whose evolution can only be explained by punctuated equilibrium such as evolution of the genus Mesohippus to Miohippus. Contrary to phyletic gradualistic belief, these genera were not ancestor-descendants, but contemporaries (Gould and Eldredge 226).

Relative frequencies

The frequency of gradualism as a mode of evolution has been observed only in 10% of organism such as trilobites. Some organisms such as mollusks have shown no degree of phyletic gradualism. It is, therefore, evident that the frequency of punctuated equilibrium as the mode of evolution is frequent in such cases (Gould and Eldredge 226).

Inductive patterns

Some organism favor punctuated equilibrium over phyletic evolution due to conducive environment. As mentioned earlier, some pelagic forms might exhibit slow and even gradualism while benthic organisms favor punctuated equilibrium. It can be inferred from evidence that punctuated equilibrium could be the mode of evolution in harsh, unstable environment while phyletic gradualism might be preferred in environments with stable niche (Gould and Eldredge 226).

Tests from living organism

Another way of proving punctuated equilibrium mode of evolution in organisms could be analyzing sister clads of modern species for morphological and genetic differences. A positive result regarding frequency of speciation and evolutionary distance might prove the theory (Gould and Eldredge 226).

Conclusion

Works Cited

Eldredge, Niles, and Stephen Jay Gould. " Punctuated equilibrium: an alternative to phyletic graduation." Models in Paleobiology. WH Freedman; San Francisco (1972): 82-115.

Gould, Stephen Jay, and Niles Eldredge. " Punctuated equilibrium comes of age." NATURE 366 (1993): 223-227.

Hull, Pincelli M., and Richard D. Norris. " Evidence for abrupt speciation in a classic case of gradual evolution." Proceedings of the National Academy of Sciences 106. 50 (2009): 21224-21229.

Monroe, Melanie J., and Folmer Bokma. " Punctuated equilibrium in a neontological context." Theory in biosciences 129. 2-3 (2010): 103-111.

Pennell, Matthew W., Luke J. Harmon, and Josef C. Uyeda. " Is there room for punctuated equilibrium in macroevolution?." Trends in ecology & evolution 29. 1 (2014): 23-32.

Saylo, Monalie C., Cheryl C. Escoton, and Micah M. Saylo. " Punctuated Equilibrium vs. Phyletic Gradualism." International Journal of Bio-Science and Bio-Technology 3. 4 (2011): 27-42.