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Punctuated equilibria at 50: half a century of stasis, cladogenesis, and macroevolutionary insights

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Review

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Introduction

Paleontologists Niles Eldredge and Stephen Jay Gould introduced punctuated equilibria (PE) to the scientific community in 1972 (Eldredge and Gould 1972). Since then, the concept has been debated and tested, misunderstood and clarified, applied, extended, and integrated into evolutionary thought. To celebrate PE's semicentennial, we and *Paleobiology*'s editors have produced this special issue. Our goal has been to bring together paleontologists, evolutionary biologists, and historians of science to reflect on the concept of PE, how it has been tested, the underlying mechanisms for stasis and punctuated change, and the broader impacts of PE for paleontology, biology, and macroevolution. In this introduction, we highlight the key components and implications of PE, briefly review the history surrounding its emergence and reception, and outline how PE expands evolutionary theory. We explain the organization of the papers included in this special issue, providing brief summaries to guide the interested reader. Finally, we conclude with a call for paleobiologists to "rediscover" PE and consider how the concept and its implications can be applied to their own work. In this endeavor, we are aware that a great many authors have contributed significant data, insight, and perspective to these issues over the years. As our purpose in this introduction is not to provide a comprehensive review, we do not cite and recognize them all individually, but we applaud all of those who have weighed in on this important topic.

Setting the Stage for a New Picture of Evolution

By the mid-twentieth century, paleontology had acquired the academic reputation as a musty, archaic science—mostly descriptive and with little to offer in the way of theory. Classes in paleontology typically involved memorizing long lists of fossil taxa, their ranges in time, and the details of their anatomy, and textbooks of the time reinforced these priorities, with detailed chapters about nearly every important fossil taxon and almost no discussion of large-scale patterns or the theoretical principles underlying life's rich history. While some (e.g., Beerbower 1968) notably looked forward to invigorating the field with new questions and new tools like geochemistry and computer modeling that could bring new insight, most followed what Stephen Jay Gould (1980a) called the "idiographic" approach to paleontology: documenting numerous small-scale facts about the fossil record (see also Gould 1986). An infamous editorial in the journal *Nature* (Anonymous 1969: p. 903) remarked that "scientists in general might be excused for assuming that … most paleontologists have staked out a square mile as their life's work." Few were interested in what Gould (1980a) called the "nomothetic" approach: attempting to synthesize broader perspectives on the fossil record and deduce laws of nature from fossils.

We look back at the 1960s as a time of social ferment, which in the United States included struggles over civil rights, the Vietnam War, and the evils of a government that seemed to be at times operating outside the law. The "question authority" attitude prevalent among the younger generation pervaded science and academia as well. Paleontology students educated in the 1960s may or may not have taken part in sit-ins and antiwar protest marches, but they were definitely revolutionaries. Many were more sophisticated than their graduate advisors regarding the latest ideas in evolutionary theory and the use of mathematics and computers, and they were eager to tackle questions and issues that were not on the menu of conventional descriptive paleontology. While steeped in the traditional approach, they drew on ideas and tools from other disciplines to ask the broad questions of pattern and process as well (Sepkoski 2012). As classic illustrations:

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David Raup (1966) embraced computer modeling to understand the array of theoretical and realized fossil morphologies; Steve Stanley (1970) used living taxa to understand how shape and sculpture influence the functional performance of (fossil) bivalve shells; and two graduate students at the American Museum of Natural History and Columbia University in New York City, Niles Eldredge and Stephen Jay Gould, asked how biological speciation theory might translate into the fossil record (1972).

No book illustrates this heady transition more than the pioneering volume *Models in Paleobiology* (1972), edited by Tom Schopf. The proposal of PE (Eldredge and Gould 1972) that appeared within is but one novel contribution among many that foreshadowed the coming revolution in paleontology. Shortly thereafter, Jim Valentine proposed a new journal to the Paleontological Society Council to highlight this new approach to the science of life's history, and the first issue of *Paleobiology* appeared in 1975. Fifty years later, it remains the premier forum for analytical, theoretical, idea-driven papers in paleontology (see papers in the 50th anniversary issue of the journal, edited by Mark Patzkowsky and Wolfgang Kiessling [2025]). Indeed, the term "paleobiology" itself was coined to emphasize the biological, theoretical side of paleontology and to move away from the old stereotype that paleontology was more like "stamp collecting," in the now-infamous words of physicist Luis Alvarez (Browne 1988).

The atmosphere at paleontology meetings during the mid-1970s was electric. Intense debate pervaded discussion on many topics, often polarized along the generational divide. Another widespread (and equally false) stereotype—that of the cool, objective, neutral scientist—was belied by occasional bad (if colorful) behavior, with people shouting at each other across the room and resorting to insults and personal attacks, both in person and in print. That scientists are human beings—passionate about important ideas and willing to go to great lengths to defend their views—can hold back progression toward the truth and understanding that they pursue. This is true not only because of ego, but also because observation is limited by prevailing views. Eldredge and Gould (1972: p. 83) argued that "the expectations of theory color perception to such a degree that new notions seldom arise from facts collected under the influence of old pictures of the world. New pictures must cast their influence before facts can be seen in a different perspective." The idea they put forward in their classic 1972 paper challenged the prevailing view of "phyletic gradualism"—that new species arise from the slow and steady transformation of entire populations over their whole geographic range (p. 84). This special issue looks back on their "new picture" of PE and how it has changed the way scientists see, collect, and interpret the data of the natural world.

The Modern Synthesis and the Emergence of PE

The new picture developed by Niles Eldredge and Stephen Jay Gould—punctuated equilibria—was among the most transformative ideas to emerge from this period of intellectual foment. The PE origin story has been recounted elsewhere in significant detail and with some remarkable personal accounts of those involved (e.g., Eldredge 1985a, 2008a, 2013, 2015, 2025; Gould 1989a, 1991, 2002; Sepkoski 2012), so here we briefly review its key elements, how they connect to preexisting theory, and its broader implications.

PE challenged the "old picture" of phyletic gradualism, where one species gradually transforms into another species over geological timescales across its entire range due to the slow and gradual action of natural selection. Instead, PE emphasized geologically rapid (relative to a lineage's total stratigraphic duration, and still gradual on ecological timescales) evolutionary change in small, isolated populations that form new species in association with lineage splitting. Small, isolated populations are much less likely to be fossilized, and only when they become common and successful are they likely to be preserved in the fossil record. Although the processes operating in those small populations are entirely consistent with Darwinian natural selection, they also accommodate the potential for chance and contingency in the origin of new species. The emphasis on lineage splitting and on the lack of significant (net) directional change within those lineages once established made possible the treatment of species as entities unto themselves, with a time of birth (splitting) and death (true extinction). These inferences are uniquely drawn from PE and call for a rather different way of reading the record of life's evolutionary history that shook up the paleontological establishment, leading to some of the more vociferous confrontations alluded to in the preceding section.

As understood for centuries, all great scientific discoveries build upon a preexisting edifice (Brooks 2011)—one can see farther when standing on the shoulders of giants. While transformative on the one hand, PE was not an invention from whole cloth; instead, it was firmly grounded in the existing understanding of evolutionary theory. The so-called modern evolutionary synthesis (Huxley 1942) of the first two-thirds of the twentieth century embodied three widely established principles (see Kearney et al. 2024) that were further promulgated by three of its chief architects: Ernst Mayr (1942, 1963), George Gaylord Simpson (1944), and Theodosius Dobzhansky (1937; see Eldredge [1985b] for discussion of the role each of these played in the development of the modern synthesis). While these principles underlie both the modern synthesis and PE, the extrapolation of pattern and process from ecological to geological timescales, and hence the implications drawn from each, differ significantly.

Allopatric Speciation

A key element of the modern synthesis assimilated by PE concerns the primary mode of speciation. Before the 1940s, most biologists assumed (as did Darwin) that gradual change within lineages (anagenesis) was largely responsible for the emergence of new species. During the 1940s, however, biological field studies and evidence from genetics showed that a crucial component of speciation was genetic isolation. Large interbreeding populations with their huge gene pools, in the absence of geographic subdivision (vicariance), seldom produced new variants. By contrast, small, isolated populations whose members were prevented from interbreeding with those of other populations often had unusual gene frequencies, and these populations appeared to be the source of most new species observed in nature. Ernst Mayr (1942, 1963) formally developed this recognition into his model of allopatric speciation (although the idea has a long history stretching back well before Darwin [1859]; see Lieberman [2000]). Mayr (1942, 1963) argued that small, isolated (allopatric—meaning "different homeland") populations on the periphery of the main population ultimately become the sources of new species. If the peripherally isolated population diverges sufficiently from the ancestral population(s) such that its members do not interbreed once they come back into contact, that population should be considered a new species. In this circumstance, the lineage splits (cladogenesis), yielding two species where there had been one.

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While the importance of allopatric speciation had come to be accepted in the biology literature and textbooks of the 1950s, most evolutionary biologists and paleontologists—then and to some extent even today—did not recognize or even question the implications of this idea for how species' originations should manifest in the fossil record (Eldredge 2008a). It is interesting to note that allopatric speciation was first proposed in 1942, yet paleontologists of that generation failed to see its implications for speciation in the fossil record for a full 30 years, until Eldredge and Gould put allopatric speciation at the center of their model. Germane here is that allopatry involves cladogenesis. Yet, before the formulation of PE, many paleontologists had focused on documenting cases of anagenesis, where the entire population of a species transformed into another species across its entire range. This view aligned with Darwin's (1859) notion of sympatric ("same homeland") transformation of species—a viewpoint superseded by the development of the modern synthesis and therefore largely outdated (Eldredge 2015). PE instead represented a natural evolution from the modern synthesis, with scholars of deep time taking the next step of asking what pervasive allopatry would look like in the fossil record. Eldredge and Gould (1972) reasoned that species should arise gradually on ecological timescales (ca. thousands of years), but that this would look "instantaneous in terms of our biostratigraphic resolution" (p. 106) on geological timescales.

Allopatry also predicts that species should arise from small populations in peripherally isolated areas, so the fossil record would be unlikely to capture the process unless that small area fortuitously happened to be preserved, and with exceptionally high stratigraphic/temporal resolution. More likely, strata would only record the presence of the descendant species once it had successfully differentiated, proliferated, and expanded its range over a much broader region, at which point it would be much less likely to show significant genetic, and hence morphologic, change. Thus, Eldredge and Gould (1972) made the case that the model of speciation almost universally accepted by biologists should yield a fossil record in which species appear suddenly over their range and without preservation of intermediate forms and then persist for long periods of time with no net morphological change.

Rates of Evolution Vary, and Some Gaps in the Fossil Record are "Real"

Because phyletic gradualism presumes that rates of evolutionary change within species are slow and steady, any intervals of apparently rapid evolutionary change observed in the fossil record were viewed as times when the stratigraphic record of "true" gradual change was incomplete. In contrast, Eldredge and Gould (1972) emphasized long periods of species-level stability—the equilibria—broken up by geologically quick episodes of speciation/cladogenesis—the punctuations (Eldredge and Gould 1972; Gould and Eldredge 1977; Eldredge 1985b, 2008a; Gould 2002). This insight, while novel, shares a connection with elements of the modern synthesis, particularly the work of another of its architects, George Gaylord Simpson (Lieberman 1995). One of the central contentions of Simpson (1944) was that rates of evolution did in fact show tremendous variation. Simpson (1944) recognized the disconnect between putative slow and gradual evolution and the extremely rapid pace of mammal evolution early in the Cenozoic, when archaic mammal groups quickly (on geological timescales) transitioned into modern mammalian orders. This rapid pace of evolution could easily be distinguished from the relatively pedestrian pace of evolutionary change that has transpired since the early Eocene—modern bats were, after all, still clearly recognizable as the kin of Eocene bats, whereas the connection between bats and archaic mammals was much more challenging to forge. Was the quick transition between archaic and modern mammals indicative of a gap in the fossil record, as proponents of phyletic gradualism would assume? Simpson (1944) argued against this view for several reasons, including the lack of evidence for such a gap in the well-studied mammalian record. Furthermore, if rates of change were truly uniform and could be characterized by the pace of evolutionary changes in bats since the early Eocene, then the amount of time missing from the mammal fossil record had to be stupendous, with modern mammal groups likely originating in the late Paleozoic. Yet the fossil record was simply not that incomplete.

To be sure, Simpson (1944) never held that long-term stasis prevailed, especially at the level of species, and he did posit that apparently sudden changes between closely related species in the fossil record were in fact attributable to gaps in the record. He further held that the fossil record could be most informative regarding changes that led to the appearance of new higher taxa, such as families, orders, etc. However, his view on rates of evolutionary change and the existence of real times of rapid evolution that could not be explained away by gaps in the fossil record in an important way set the stage for a key insight of Eldredge and Gould (1972): rates of evolution vary, and seeming morphological gaps or disjunctions separating ancestral species from their descendants in the fossil record might not be caused by an incomplete fossil record.

Emerging Hierarchies of Evolutionary Entities

A final crucial aspect from the modern synthesis that helped set the stage for the development of PE was Dobzhansky's (1937) acknowledgment that nature was hierarchically arrayed, and processes at a lower level could not necessarily be extrapolated to explain what happened at a higher level (Eldredge 1985a,b, 2008b; Gould 1985). Dobzhansky (1937) detailed this view by explaining that evolution at the grand scale was more than just genetic mutation (Eldredge 1985b, 2008b, 2015; Gould 2002). Instead, genetic mutations need to spread within the context of populations, and different processes govern the appearance of mutations in organisms and the spread of those mutations through populations. Dobzhansky (1937) eloquently explained this as the difference between the physiology of organisms and the physiology of populations (Eldredge 1985b, 2008b). Further, both Dobzhansky (1937) and Mayr (1942) held that species were real entities at any one time, despite being evanescent and continually changing through time. A novel insight of PE was that not only were species real at any one time, but they were also real and persistent through time (Eldredge 1979, 1985b, 2008b; Gould 1982, 1985, 2002; Turner 2017). Just as the processes affecting mutations within organisms and the spread of organisms within populations mattered, so too did the processes involving the appearance and disappearance of species. Again, this novel insight was connected to past discoveries, and it would have fundamental implications for evolutionary theory.

The existence of hierarchically arrayed biological entities that both underpinned and emerged from the modern synthesis was buttressed by work in phylogenetics, a field profoundly burgeoning around the time of the development of PE (see discussions in Eldredge [2011], Wiley and Lieberman [2011], and Brooks et al. [2021] and references therein). As the field of phylogenetics grew, it became clear that higher taxa could not give rise to other higher

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taxa. Not only would this violate the principle of monophyly, but there was no process of "familification" or "generification" (Hendricks et al. 2014). It might seem paradoxical today, but the architects of the modern synthesis were operating within a framework that posited that evolutionary change not only produced new species, but also new genera, new families, orders, etc. And these categories were invoked to convey not just the order of evolution but the degree of change. This aspect of the modern synthesis is completely nonsensical today and has been entirely discarded. While phylogenetics as a field in the early 1970s did not provide consensus or unanimity on the nature of species, and still does not, the rejection of higher taxa as evolving entities does align well with PE's emphasis on the centrality of species.

Eldredge and Gould were well versed in the new developments in genetics, paleontology, and systematics that comprised the modern synthesis when they arrived at Columbia hoping to study evolution in the fossil record (Eldredge 1985a, 2008a; Gould 1989a, 2002; Allmon 2008). Yet, as Eldredge (1985a) recalled, his research on phacopid trilobites (Eldredge 1971) did not reveal the expected pattern of slow continuous transformation called for by the old view of phyletic gradualism. Instead, each species appeared at a particular level in the fossil record and then remained largely stable ("stasis" in the parlance of Eldredge and Gould [1972]) through strata spanning millions of years. Putting the pieces together from their understanding of allopatry, the fossil record, and species as the only "real" entities in systematics ultimately led Eldredge and Gould to see the inherent contradiction between contemporary speciation theory and the classic notion of phyletic gradualism and to propose their alternative of PE. Eldredge and Gould (1972), then later Gould and Eldredge (1977), and a large number of other studies, showed that only rarely does the fossil record produce "insensibly graded sequences" (Eldredge and Gould 1977: p. 39) of organisms gradually changing through time as they evolved into new species.

Early Reactions to Eldredge and Gould's (1972) Landmark Paper

Eldredge and Gould (1972) eventually became among the most cited papers in the history of paleontology, garnering an incredible 7557 citations (as of 26 August 2025, according to Google Scholar). The paper is a masterpiece of writing and incisive thinking that raises a number of interesting and compelling issues. The opening discourse on the philosophy of science points out that all scientists are products of their time and culture and hence are biased to see what they expect to see. Darwin had led paleontologists to expect phyletic gradualism, which they tried mostly in vain to document for more than a century. We are not aware of any other scientific paper written before this time that began with such an exegesis of the theory behind the very nature of scientific ideas and how they come to be adopted over time.

Not only is Eldredge and Gould (1972) one of the most cited paleontological papers, but by the mid-1970s it was also one of the most controversial. Like the best of all scientific proposals (e.g., Alvarez et al. 1980), it triggered a flood of literature attempting to either support or refute PE's predictions. One of us (D.R.P.) vividly remembers attending the Second North American Paleontological Convention in Lawrence, Kansas, in the summer of 1977, a meeting that exposed him to the full spectrum of ideas and personalities in paleontology. Several sessions touched on the PE debate, with passionate arguments from both critics (e.g., Art Boucot, Phil Gingerich) and defenders (Gould, Eldredge, and Steve Stanley) alike. It was an eye-opening experience to see such a major scientific debate played out on the stage in front of the entire profession of paleontologists. Such lively debates over PE continued at meetings well into the 1980s, for example, with results interpreted to support stasis being challenged as merely evidence of "gradualism at zero rate."

That PE received such strong pushback from proponents of the modern synthesis is surprising, given that it grew from ideas central to that very theory. The arguments over PE centered on a few points, which Gould and Eldredge (1977) nicely summarized on the fifth anniversary of the paper's release. A particular point of contention was the argument that stasis was much more prevalent in the fossil record than had been previously supposed. Supporters maintained that the geological literature was one vast monument to stasis. For example, if species did not appear suddenly in the fossil record and remain relatively unchanged over their durations, then biostratigraphy would never work—and yet almost two centuries of successful biostratigraphic correlations were evidence of just this kind of pattern (Eldredge and Gould 1977). Paleontologists had been trained that evolution was gradual, the record was full of gaps, and therefore stasis was simply a non-result that could be ignored rather than treated as something of interest. Gould and Eldredge (1977) famously championed the idea that "stasis is data" (p. 116), asking paleontologists to reconsider the record of morphology over time and what it might be telling us. They and their supporters argued that stasis indeed was far more pervasive than had been thought; as stated by Gould (1980b: p. 181): "The extreme rarity of transitional forms in the fossil record persists as the trade secret of paleontology."

The issue is what LCI and MMY recall Stephen Jay Gould often describing as a relative frequency argument. He and Eldredge in their many works acknowledged that the spectrum from phyletic gradualism to PE is likely to be fully populated and represented in the immensity of the fossil record. But what matters for setting the course of life's evolution, and the implications we can draw from it, is *which is most common.* They maintained that, if the allopatric model is how most species come into existence, as argued by the modern synthesis, then documented cases of gradualism in the stratigraphic record should be rare in comparison to those showing stasis and punctuation. Gould repeatedly emphasized this point throughout his career, and both Gould and Eldredge encouraged their students to use the fossil record to assess the frequency of PE versus gradualism. P.H.K.'s Ph.D. thesis, for example, was designed to test the relative frequency of PE in the Maryland Miocene molluscan fauna, and an aspect of B.S.L.'s Ph.D. thesis tested this question in the Devonian of the Appalachian Basin. Robust datasets of temporal patterns in morphology are time-consuming to generate, and fewer well-documented cases exist than one might suppose. As well, statistical analyses of those data can and have been interpreted in different ways by different researchers. Nevertheless, it seems increasingly apparent that PE wins out over phyletic gradualism in the critical question of relative frequency. Interestingly, there are suggestions that some taxa or some environments are more likely than others to exhibit one pattern over the other, which if substantiated will lead to even deeper insight about evolutionary processes in space and time.

How PE Expanded Evolutionary Theory

The Connections between Microevolution and Macroevolution

While PE was an idea that focused on the fully formed appearance and persistence of species through time in the fossil record, it also

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became something more, for several reasons. First, in the paper itself, in a section titled "Some Extrapolations to Macroevolution," Eldredge and Gould (1972: pp. 108–112) attempted to forge broader connections to patterns and processes of evolution. They specifically distinguished their view of macroevolution based on PE from that of the modern synthesis, which maintained that macroevolution was *only* the product of extrapolated population genetic phenomena that yielded gradual change and "stately unfolding" (Eldredge and Gould 1972: p. 109) over time. Because PE's central contention, stasis, entails that species are mostly stable over millions of years, the standard selection processes impacting organisms and populations on ecological timescales generally do not induce much change in species on geological timescales. If species are real and persistent entities over geologically long intervals of time, as Eldredge and Gould (1972) posited, then they become important units of evolution. The relative prevalence of PE has important implications for the debate about whether the processes of microevolution (evolution below the species level) can be smoothly extrapolated to explain macroevolution (evolution at and above the species level). (See Erwin [2000, 2010], Gould [1982, 1985, 2002], Myers and Saupe [2013], and Kearney et al. [2024] for extensive discussions on the relationship between micro- and macroevolution.)

Disparity and Trends

Eldredge and Gould (1972) specifically distinguished two important macroevolutionary phenomena that needed to be revisited in light of PE. The first was "'classes' of great number and low diversity," such as major clades of echinoderms that evolved early in the Paleozoic (Eldredge and Gould 1972: p. 110). In modern parlance, this phenomenon would be treated as a question about the difference between diversity and disparity (Gould 1989b). PE informs this discussion by emphasizing that morphological change is concentrated at the time of speciation. In this view, speciation events might each encompass small or large amounts of change, and very large morphological shifts can be accommodated in very little geological time with a quick succession of speciation events. This interesting phenomenon eventually led to Gould's (1989b) work on the Burgess Shale and the tremendous amount of literature it inspired about the nature and significance of Cambrian soft-bodied faunas. It also produced important interactions between paleontology and the newly emerging field of evolutionary developmental biology (e.g., Erwin 2017). Thus, PE helped create links (although not the only ones) to macroevolutionary processes emanating from developmental systems.

The second important macroevolutionary phenomenon distinguished by Eldredge and Gould (1972: p. 111) was the nature of trends. They argued, building on the work of Wright (1967), that "just as mutations are stochastic with respect to selection within a population, so might speciation be stochastic with respect to the origin of higher taxa." In this respect, macroevolutionary trends are explained by the differential origination and extinction of species. This view is very different from that of the modern synthesis, which saw trends as gradual directional change resulting from consistent selection pressures on individuals within lineages (Eldredge 1979, 2015). While Eldredge and Gould (1972: p. 112) suggested that such stochastic speciation followed by sorting involved "no 'new' type of selection," Stanley (1975) reasoned that such trends could indeed involve a new type of selection and coined the term "species selection." Despite this connection, the original formulation did not require that species selection occur for PE to be valid. (For extensive discussions of species selection, see Vrba [1984], Gould [2002], Lieberman and Vrba [2005], and Jablonski [2008].)

From Single Species to Regional Biotas: PE, Turnover Pulse, and Coordinated Stasis

Another way that PE expanded its scope beyond evolutionary patterns and processes within individual lineages was in the development of the turnover pulse hypothesis (Vrba 1985) and coordinated stasis (Brett and Baird 1995; Brett et al. 1996; Morris et al. 1995; see also Brett et al. [2025] this issue). These related hypotheses of pattern and cause extended PE beyond the evolution of single species to argue that groups of species co-occurring in regional biotas show roughly coeval origins, long periods of coincident relative stability (Miller 1997), and roughly coeval extinctions and extirpations. These authors suggested that comparatively large shifts in the physical environment drive coordinated pulses of turnover across regional biotas, and Morris et al. (1995) further proposed that aspects of ecological structure helped to maintain relative stasis between turnovers. Elements of these hypotheses were incorporated in Eldredge's (2003) "sloshing bucket" hypothesis, which emphasized the important role abiotic environmental change played in driving evolution.

PE as a More Universal Phenomenon—Extending beyond the Fossil Record

Another fundamental way that PE became distinguished is as a broader, more general theory that might serve as a metaphor for describing, and perhaps helping to explain, the way that change occurred in a variety of systems, not only evolutionary and paleontological, but also, for example, cellular, ecological, and cultural (Gould 2002; Atkinson et al. 2008; Valverde and Solé 2015; Wosniack et al. 2016; Blanco et al. 2021; Duran-Nebreda et al. 2024; O'Brien et al. 2024; Douglas et al. 2025). And, in this respect, PE also helped forge important connections between paleontology and neontology, as many neontologists set out to test aspects of the theory (Eldredge et al. 2005), including developing novel approaches to characterize molecular and phylogenetic changes (Pagel et al. 2006; Bokma 2008; Wada et al. 2013; Garcia-Erill et al. 2024). Clearly, PE sparked a fundamental reimagining of the causal levels and processes of evolution, and it continues to inspire a new generation of evolutionary biologists more than 50 years after its inception.

A Golden Jubilee: Papers of This Special Issue Commemorating the 50th Anniversary of PE

Models in Paleobiology, the volume that included the groundbreaking Eldredge and Gould (1972) paper "Punctuated Equilibria: An Alternative to Phyletic Gradualism," was based on a symposium held at an annual meeting of the Geological Society of America (GSA). Likewise, most of the papers in this issue developed from a topical session held at GSA in October 2022. We convened this daylong session, entitled "Punctuated Equilibrium: 50 Years Later," to commemorate the 50th anniversary of Eldredge and Gould (1972), reflect on PE's history and influence, and showcase work that continues to address unresolved issues in new ways and with new datasets. Attendees were privileged to hear from PE cofounder Niles Eldredge, paleontologists who conducted some of the earliest work on PE, various students of Eldredge and Gould (including each of us), and newer voices in the field. The papers in this special

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issue represent several themes: historical perspectives, the state of the evidence regarding PE, mechanisms of stasis and PE, and broader theoretical perspectives building on PE.

Historical Perspectives on PE

Fortunately for all, Niles Eldredge was able to attend and speak at the 50th anniversary celebration of PE, and thus very appropriately, Eldredge (2025) leads off this commemorative issue by briefly recounting how he and Stephen Jay Gould came to coauthor their 1972 paper, while providing an exegesis of the principles and data underlying PE. As related earlier, key elements of PE are that speciation primarily occurs in the allopatric mode and that most species display stasis throughout much of their histories—elements derived from data in both extant biota and the fossil record. Notably, Darwin's early views on the origin and evolution of species were well aligned with the prevalence of both allopatry and stasis, although Darwin later came to embrace a view that emphasized sympatric divergence and gradual change. Eldredge (2025) discusses the important role that geographic factors play in mediating PE, both via the phenomena that trigger allopatry and the mechanism of stasis that involves the geographic structure of populations within species, such that each population experiences somewhat different selection regimes (see also Kelley et al. [2025] in this issue). Another important aspect is how PE is fundamentally connected to the hierarchical structure of nature, where changes at one level, the genome, do not necessarily directly extrapolate to changes at higher levels like the organism or the species. PE especially helped validate the view that many trends arose from the differential birth and death of species. Eldredge (2025) further describes the important extension of PE whereby not only single individual species lineages show stasis and change, but many species that occur together within a broader region have largely concurrent patterns of speciation and extinction, bracketing long intervening periods of stasis (see also Brett et al. [2025] in this issue on this concept of "coordinated stasis")—which points out the need to understand the broader environmental and ecological context of change that affects groups of species.

Dresow (2025) argues that Gould, at an early stage of his career, suggested that organisms were continually improving through time and held a commitment to the "adaptationist programme"—both concepts that Gould later spent much time criticizing. Dresow suggests that, over the decades after the publication of the 1972 PE paper, a number of factors led Gould to abandon his earlier positions and reject beliefs he held earlier in his career. Although Gould (2002) claimed that PE was the "coordinating centerpiece" of his life's work, Dresow posits that Gould's conceptual framework changed over the years (Lieberman and Vrba [2005] and Lieberman and Eldredge [2024] provided examples of this in other instances as well).

Yacobucci et al. (2025) conducted an exploratory survey to understand perceptions of PE by paleontologists and evolutionary biologists, including students and professionals. Although those who responded to the survey recognized the importance of PE, instructors typically spent a week or less on the topic in their courses, and misconceptions and inconsistencies in their understanding were noted (e.g., that anagenesis is common). Yacobucci et al. (2025) recommend pedagogical strategies for improving students' understanding of PE and ways to expand on this pilot survey.

The State of the Evidence Regarding PE

Stanley (2025) discusses various tests of data sets, some of which he had previously used to test the validity of the PE model. These include the "test of adaptive radiations," which shows that species in several families (his examples include mammals and bivalves) show stasis for millions of years, far too long for phyletic gradualism to explain their duration. Stanley also recaps his "test of living fossils," which predicts that long-lived clades that experienced very little branching and diversification would be expected to show extreme stasis and look much like their ancestors—as they do. Stanley reviews a number of recent multivariate morphometric studies of fossils through long time intervals, most of which show stasis and almost no gradualism. Finally, he points to some recent examples documenting rapid speciation in modern organisms, which was predicted when the allopatric speciation model was the original basis for the PE model in 1972.

Lieberman and Strotz (2025) examine studies of evolutionary change explicitly designed to test the hypothesis of PE published between 2008 and 2023. Papers reviewed include new analytical methodologies and techniques applied both to the fossil record and extant organisms. They find that the preponderance of work indeed documents stasis and cladogenesis, thus supporting the ubiquity of PE and the relative frequency argument of Gould. Authors who concluded that their studies did not support stasis employed a different, narrower definition of stasis, treating nondirectional morphological fluctuations as at odds with stasis, rather than the definition used by Eldredge and Gould (and many others) that considered stasis as little to no net change over the duration of a species.

Hunt et al. (2025) analyze the state of the evidence for and against PE since the 1972 paper that started it all. They point out that a rigorous statistical method is needed to truly determine whether fossil lineages show stasis, gradual directional change, a random walk, or something else. Using statistical methods already developed by Hunt, they find that there were very few cases of gradual directional change among the dozens of studies that have been published over the last 50 years, whereas stasis is by far the most common pattern, along with random walks. However, these authors argue that more data are needed to show that morphological change is concentrated in pulses associated with speciation.

Anderson and Allmon (2025) argue that PE continues to be misunderstood, and in cases dismissed, by some evolutionary biologists, in part due to confusion about what is meant by "mode" of evolution, that is, cladogenesis and anagenesis. If cladogenesis is the dominant mode by which species originate, as proposed by PE, ancestors should persist along with their descendants. They test this hypothesis by examining recently published phylogenies for 30 clades (invertebrates, vertebrates, and radiolarians). Importantly, they find cladogenesis to be the most prevalent mode of species origination based on the "persistence of ancestor" criterion, thus supporting the dominance of PE (see Strotz and Allen [2013] for a detailed demonstration that this is often the case in forams as well).

Documenting long-term stasis in fossil species requires accurate estimates of their stratigraphic duration and, therefore, that morphology can be tied to specimens with explicit relative stratigraphic position and age. Hendricks and Lieberman (2025) highlight how important it is to document species durations using fossil occurrences that are supported by museum voucher specimens. They illustrate the problem by showing how various online and published databases give different first and last occurrences for the trilobite *Eldredgeops rana* (Green, 1832) and its family, Phacopidae, which leads to varying estimates of the duration of stasis in this species (although all imply durations of many millions of years). Hendricks and Lieberman (2025) encourage the paleontological

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community to identify stratigraphic voucher specimens for fossil occurrences in museum collections and place photographs of these specimens in publicly accessible websites. This will facilitate a dramatic increase in the number of studies that can test for stasis and thereby assess PE.

The end of the Pleistocene ice age resulted in major changes to North American environments, which might be predicted to result in anatomical changes in vertebrate species, including decreased body size and changes in morphology. Syverson and Prothero (2025) use recalibrated dates and a new bootstrap method for estimating ages in a time series, in combination with morphological data, to document morphological stasis in multiple bird and mammal species from the famous Rancho La Brea tar pits in California. They uncovered stasis in the overwhelming majority of species. Moreover, the very few significant morphological changes recognized did not correspond to times of climate change, highlighting the complex relationship between late Quaternary climate and evolutionary responses.

Wagner and Wright (2025) test PE using phylogenies. They point out that existing models of trait change assume a constant distribution of rates over time, whereas PE explicitly calls for elevated rates of change in association with cladogenesis and low rates thereafter. They therefore model character change as dependent upon the number of branching events rather than elapsed time and show that, for strophomenoid brachiopods during the Ordovician radiation, punctuational models are strongly favored over continuous ones. As rates of morphological change are tied to branching, their model is also better able to capture the high disparity often seen early in a clade's history.

Mechanisms of Stasis and PE

The prevalence of evolutionary stasis within species lineages is one of the key aspects of PE. Kelley et al. (2025) argue that one way stasis can arise is through the variable evolutionary responses triggered by ecological interactions of predators and their prey and hosts and their parasites in geographically structured populations. In a process termed "coevolutionary alternation," local populations experience different coevolutionary dynamics (e.g., involving changes in predator preferences and prey defenses), as well as different physical environments. This geographic mosaic of biotic interactions, selection pressures, and the resultant spatial variation in coevolutionary trajectories can produce stasis on the scale of entire species. Kelley et al. (2025) discuss the difficulty of modeling coevolutionary alternation and testing it as a potential cause for stasis. They argue that coupled stochastic differential equations will represent a useful way of modeling time series to better understand the effects of predator–prey and host–parasite interactions on selection pressures and morphological stasis and change, and they present a framework for how such modeling might be accomplished.

The classical approach to testing for PE entails the study of morphology over time within a lineage. Slattery et al. (2025) adopt this approach in their study of nuculid bivalves, but they do so explicitly in the context of environmental change to assess the potential role of the physical environment in generating stasis. Sheldon's (1996) "Plus ça change" model predicts stasis in settings characterized by substantial environmental variability but anagenesis when the environment is more stable and adaptation can keep pace with any slow variation. They find significant morphological change during the stable warm Cretaceous and demonstrate stasis during the more variable "icehouse" conditions of the Neogene–Quaternary, supporting hypotheses that causally relate evolutionary mode to environment.

Polly (2025) also investigates the role of environment in setting the pace of morphological change within a species using a set of models to simulate sea-level change, population size and fragmentation, and morphological change in Bermuda land snails that approximate the *Poecilozonites* Boettger, 1884 used in Eldredge and Gould (1972) (see also Gould 1969). He shows that glacial/interglacial-scale changes in sea-level drive changes in morphology by fragmenting and isolating small populations during highstands and uniting populations across a broader area during lowstands. Genetic drift during highstands fosters rapid morphological change in small isolated populations, but lowstands enable the population to coalesce and grow, damping the potential for change. Further, he shows that the sedimentary record itself can influence the interpreted pattern of stasis and rapid change, because sea-level rise (in simulated Bermuda) is more likely to be characterized by expanded sedimentary sequences, while lowstands correlate with pedogenesis and a comparatively thin stratigraphic record. In this case, depositional patterns make it easier to document gradualism, because times of comparative stasis are characterized by thin stratigraphic sections, while times of genetic drift are recorded in thick sequences of aeolian sedimentation. That it was possible to document stasis despite this bias, argues Polly (2025), provides even greater support for the PE pattern.

Casanova (2025) examines molecular mechanisms that could explain the key patterns of PE—long-term species stasis and the concentration of evolutionary change at speciation. Analyses of patterns of variation within developmental regulatory genes show that they also display long periods of little change, punctuated by relatively rapid changes associated with cladogenetic events. Casanova (2025) uses principles from game theory, along with simulations, to illustrate how changes in developmental regulatory genes and their dosage provide a molecular mechanism to explain PE. She argues that long periods of stasis and relatively rapid periods of evolution emerge due to the existence of stable gene networks that are in turn subjected to ongoing neutral and adaptive molecular changes occurring all the time. These networks are moreover buffeted by occasional substantial perturbations to the physical environment that organisms variably experience, facilitating rapid change and cladogenesis.

Broader Theoretical Perspectives Building on PE

Tëmkin (2025) discusses the relationship between PE and hierarchical approaches to evolutionary biology. Biological entities such as genes, organisms, and species are nested from smaller to larger levels and interact in complex ways. Patterns and processes at any lower level cannot necessarily be extrapolated to determine what happens at a higher level. PE validated the notion that species are important biological entities that persist for long periods of time and need to be better incorporated into evolutionary theory. Tëmkin (2025) elaborates on the differences between entities in the ecological/economic hierarchy and the reproductive hierarchy and explains how these hierarchies interact. Tëmkin (2025) further argues that the nature of the hierarchical system, along with interactions between entities and the physical environment, determines when entities persist and when they change.

Brett et al. (2025) reexamine the concept of coordinated stasis: the idea that groups of evolutionarily stable species also demonstrate a degree of ecological stability in their associations, with stable ecological evolutionary subunits (EESUs) separated by

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geologically brief periods of rapid change between EESUs. The study expands the scope of coordinated stasis beyond the classic example from the Middle Devonian Appalachian Basin and, with additional Late Ordovician examples, finds that EESUs and their boundaries were coincident over broad areas (provinces and even beyond). The authors attribute large-scale faunal turnovers to widespread habitat degradation leading to isolation of marginal populations that promote coordinated episodes of speciation, extinction, and migration—a process consistent with PE.

The Future of PE—Musing on the Next 50 Years

As the history of the world unfolds, similar phases seem to repeat, while elements also change materially. The same observation holds for our understanding of Earth history—Gould (1987) made this very point in his book *Time's Arrow, Time's Cycle* (explored in greater detail in Lieberman and Eldredge [2024].) Like Earth history, the reception of PE shows a trajectory that is both cyclic and progressive. It has moved in and out of vogue based on Google Scholar citations, which oscillate up and down every few years. Further, there has been definite progress in its reception by the scientific community, including in the realm of paleobiology, where it has attained nearly canonical status. Gould and Eldredge (1986) remarked two dozen years after its inception that PE had reached the "third stage" of knowledge. They quoted Von Baer (1866: p. 63), who in turn quoted Louis Agassiz, "when a new doctrine is presented, it must go through three stages. First, people say that it isn't true, then that it is against religion, and, in the third stage, that it has long been known" (Gould and Eldredge 1986: p. 143).

Although we will not repeat Gould and Eldredge's (1986) exegesis in detail, PE has certainly gone through these phases. It was first viewed as highly controversial, especially among certain evolutionary biologists, then denounced by some as almost heretical (against Darwinism, for instance), and then later assimilated into what was viewed as the preestablished baseline of paleobiological and evolutionary knowledge—in this case as "the necessary and logical outcome of what the Modern Synthesis always knew" (Gould and Eldredge 1986: p. 143). The fact that such a trajectory can even be identified speaks to the notion that a series of contingent events, in this case regarding the history of the reception of a scientific idea, can in fact display elements of predictability (see Lieberman and Melott [2013] and Lieberman and Eldredge [2024] for how contingency can be compatible with predictability).

Several papers in this special issue (e.g., Anderson and Allmon 2025; Hunt et al. 2025; Lieberman and Strotz 2025) explore how the general tenor of support for PE, on the occasion of its 50th anniversary, has progressed since attaining the "third stage." And PE has largely fared well; no longer is there much of a "battle" (see Lieberman and Eldredge 2014) surrounding whether one should accept or reject PE, despite a tendency for revisionist history and tendentiousness to be rewarded in modern culture. Nevertheless, support or opposition to PE is somewhat of a proxy for a continually re-emerging debate about the relationship between micro- and macroevolution (Kearney et al. 2024), so we do not expect the controversy surrounding PE to ever fade completely. Further, important research inevitably remains to be done, and support continually needs to be provided. One should not expect otherwise, as Shallit (2005: p. 2) rightly quoted (in translation) the famous German philosopher Schopenhauer's (1818: p. xxv) statement that "to truth only a brief celebration of victory is allowed between the two long periods during which it is condemned as paradoxical, or disparaged as trivial."

As mentioned, predictability is at times possible, even for the drama surrounding scientific ideas. As a callback to the "Quo Vadis?" section of Gould's (1980c: p. 128) classic paper, which in turn is a callback to John 13:36 from the New Testament, where Simon Peter asks Jesus the same ("Whither goest thou?") at their final meal before Jesus faces arrest, trial, and crucifixion, we briefly augur how things might change during PE's second half century. First, we anticipate that mechanisms of stasis and related insights will be one of the most important areas of research in evolutionary biology (e.g., see Kelley et al. 2025). Second, the number of PE studies based in neontology, especially the association between molecular change and cladogenesis (e.g., see Casanova 2025), will continue to ramp up and offer promising areas of research. This points to the important bridge that PE—and the journal its success helped shepherd into existence, *Paleobiology*—forged between those who study extant and extinct organisms; the divide between the two no longer seems as distinct as it once was, and this will benefit both disciplines, even as it blurs their edges. We anticipate that the theoretical insights and extensions made possible by PE in the area of macroevolution, as well as fields well beyond paleobiology, are certain to expand in both breadth and impact.

Unfortunately, third, misunderstandings about the meaning of PE are certain to continue. Today (and likely in the future), such misunderstandings are mostly manifest in studies that have also modified the definitions of stasis and PE relative to how they were expressed by Eldredge and Gould. Changes in definition are not necessarily all bad, as long as they are well explained and well supported. However, reading only the studies that have redefined PE and stasis risks a lack of understanding that will frustrate communication and ultimately inhibit scientific progress, as different scientists will be talking about different phenomena in the same breath. This unfortunate potential scenario speaks to the need for scientists to always retain some connection to the primary literature on major theoretical concepts. Proper scholarship can avoid misunderstandings that sometimes take decades to resolve in the scientific literature.

Hence, we close with a plea to teach PE (see Yacobucci et al. 2025) as a fundamental element of college biology and geology classes. Importantly, such courses should include reading the original text of Eldredge and Gould's (1972) paper whenever possible. The paper serves not only as an exposition of how to think about evolution in the fossil record, but also as a model for big and bold thinking and lucid and persuasive writing. The paper partly succeeded because it contained discussions germane to so many areas, including not only the nature of species and speciation in the fossil record, but also the connections between theory and data and the very philosophy of science itself. As long as paleobiology remains a field where big and bold ideas like PE are encouraged, we predict a bright and thriving future. As a final prediction, there *will* be a centenary celebration commemorating PE in this journal—the interest the paper generated, the great number of studies in so many different areas it inspired, and the fact that its development eventually led paleontologists to be called back to the "high table of evolution" (Maynard Smith 1984; see Eldredge 1995) are sure to continue to resonate across the decades. Regrettably (ancillary prediction), none of us likely will be able to attend that centenary celebration. We therefore here acknowledge how PE, along with other works by its architects Niles Eldredge and Stephen Jay Gould, has shaped the present-day scientific careers not only of us guest editors, but of countless others. May it continue to do so for paleobiological generations to come.

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