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Reflections on punctuated equilibria

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Article

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It is a pleasure to be invited to contribute to the celebration of the publication of "punctuated equilibria" ("punk eek") 50 years ago—the canonical version I did with Steve Gould (Eldredge and Gould 1972) at the behest of Tom Schopf for his visionary project to inject more thought, more interpretation and theory, into the working lives of paleontologists.

Steve was determined to be a part of Tom's plan to do a GSA symposium and publish a book of essays on this new-fangled concept of "paleobiology." Tom had a list of topics and was shopping around for speakers to be assigned to each one. When Steve saw the list, he told me that he had first wanted "morphology"—but that was already assigned to Dave Raup. So he opted instead for "phylogeny"—but that had been grabbed up by Mike Ghiselin. That left only "speciation," the last of the evolutionarily imbued topics on Tom's list, as yet unassigned. Steve called me up, explained the situation, and said he had settled for speciation—but could not think of anything much to say about it beyond the manuscript I had written and recently submitted to *Evolution*—there of course being no *Paleobiology* as yet. "The Allopatric Model and Phylogeny in Paleozoic Invertebrates"—a distinctly un-Gouldian, plodding, if accurate, title (Eldredge 1971). Without Ralph Gordon Johnson in the editorial chair of *Evolution* at that time, I doubt that that early paper would have been accepted. As it was, it was likely to have gone relatively unnoticed—had not Tom come along, Steve grabbing "Speciation"—and Steve asking if we could coauthor the paper along the basic lines of my first effort. He was stuck with "speciation," and couldn't think of anything much to say beyond what I had said in the *Allopatric Model* manuscript.

We had known each other since 1963, when Steve (and Bud Rollins and seven or eight others) showed up for graduate work at Columbia. I was a college junior and an eager, wannabe paleontologist at that point—freshly back from a summer in Brazil, taking baby steps in ethnography, while prying Pleistocene invertebrate fossils out of the sandstone unit that formed a natural harbor for Arembepe's fishing boats. All the while thinking I'd rather "Speak to the Earth, and It Shall Teach Me" (paraphrasing Job's admonition carved into Indiana limestone over the Schermerhorn Hall portal where geology, plus zoology, anthropology, fine arts, and psychology were all crammed together) than to ask personal questions of people whose language I spoke only haltingly. I stupidly imagined that paleontology was the gateway to evolutionary biology—a mistaken assumption it turns out that I am very glad to have made.

Tom accepted the arrangement—though given his fierce dislike of our paper (still palpable in his editorial introduction), he had no real idea what was coming from us. Steve suggested that I be senior author, and he would deliver the GSA symposium address—as I (Steve said) did not like giving talks (which was very true). And, after a brief later tussle, that was how things stood.

The GSA remains in this early Ur storyline, as the "son of Punk Eek" follow-up paper, published in *Paleobiology* five years later (Gould and Eldredge 1977), was hashed out in its final form at the GSA meeting in Denver in 1976 in Steve's hotel room overlooking Mile High Stadium. Steve had written an extensive draft. My main contribution to that effort, apart from helping to compile literature that largely complained about our initial endeavor, was to insist that everywhere Steve wrote "tempo" he MUST add "and mode." Including in the title: "Punctuated Equilibria: The Tempo and Mode of Evolution Reconsidered." I insisted on this, not just out of some sort of deference to George Gaylord Simpson's 1944 book title, but because Simpson had pointed out that speciation—as opposed, for example, to phyletic evolution—was indeed a distinct mode of the evolutionary process.

So what was/is "punctuated equilibria"? Originally, in 1971, it was simply as my turgid title said it was: as I have been recently putting it on the august pages of Twitter, Punctuated Equilibria = Allopatric Speciation + Stasis.

In PE 1.1—the Schopf canonical version—the main substantive addition over the 1971 paper that has proven to have had legs is centered on the explicit ontological vision of species that emerged as we looked for a way that directional trends in evolution could be reconciled with what we claimed to be the predominant pattern of within-species evolution: stasis. Meaning that in most species, sampled individuals near the end of the stratigraphic range tend to look very much like the earliest known samples of that species lineage. There is within-population variation, as well as geographic variation: we never thought stasis meant absolutely rigid non-change. Yet we alleged that temporally well-sampled species did not tend to show

much accumulated phenotypic change throughout their known histories—even as those histories entailed millions of years. Especially long periods of time involving marine organisms—especially the abundant marine invertebrates with which we had our own personal experiences. (Yes—I admit Steve's thesis was on Pleistocene Bermudan land snails—but he was well imbued with the scene our mentors, Norman D. Newell and Roger L. Batten, represented: the history of marine invertebrate life in the epicontinental seas of yore—perhaps soon to be revisited upon us with the accelerating threat of global warming) (Fig. 1).

Steve came to call "stasis" paleontology's "trade secret." We didn't know it at the time, but the 30-year-old Darwin had also seen punctuated equilibria—and saw that if most evolutionary morphological change occurs in geographic isolation with the emergence of new species, the problem of stasis disappears. Much as we still do today, Darwin saw species as entities whose component organisms engage in sexual reproduction but, with the exception of relatively rare cases of full-fledged hybridization, are unable to reproduce with members of other species—no matter how closely related. And he saw that geographic isolation is a common condition and causative agent of evolutionary change. He had his own data on that—mainly from archipelagos (the Galapagos, of course—but before that, the two Falkland/Malvinas Islands, and the southern Chilean coastal islands around Chiloe).

But Darwin knew of no data that supported the type of gradualism that his hero Lamarck had been promoting ever since his monograph on marine invertebrates of 1801. Nonetheless, for reasons I'll mention later, Darwin rejected punk eek in favor of the predominant causative power of the passage of time over differentiation engendered by space.

I am speaking of the young Darwin, and his entries in his famous *Transmutation Notebooks B–E*, written between 1837 and 1839, after he had returned to England in late 1836, after 5 years of seasickness on the *Beagle*, when he saw the things that led him to his theories of mountain building (he saw the evidence that the Andean central volcanic belt had been present above sea level well before the sediments of the foreland basement had been consolidated and uplifted [Aconcagua!]); his related theory of coral atoll formation; and, of course, his transmutational theory of the history of life.

The first *Transmutational Notebook, Notebook B*, was where Darwin first dealt with adaptation (instead of the replacement in space and in time of ancestral species by descendants—the original conceptualization of transmutation and the origin of species). Darwin says there will prove to be a law involving inheritance that will yield a scientific explanation of how morphology and/or species evolve. But, lacking that, in *Notebook B*, he could specify two conditions: space and time, which set the conditions, or are the arenas, for evolutionary change.

By *Notebook D*, a year later, he had formulated that law: natural selection. In *Notebook E*, Spring 1837, Darwin returns to his thinking regarding space and time and evolutionary change with this stunning single-sentence paragraph:

> If separation in horizontal direction is far more important in making species, than time (as cause of change) which can hardly be believed, then uniformity in geological formation intelligible. (p. 135 in original pagination)

Translated, we get:

> If separation in horizontal direction [*allopatric speciation*] is far more important in making species, than time [*phyletic gradualism*] (as cause of change) which can hardly be believed, then uniformity in geological formation [*stasis*] intelligible.

I didn't stumble on all this until the early 2000s, when I was working on the AMNH *Darwin Exhibition* and got to know and work with historian David Kohn. David had published his annotated studies of the texts of Darwin's *Transmutation Notebooks* in 1987. I had remained blissfully unaware of them. I am not sure about Steve—who of course saw everything. But I do not think that Steve took any note of this particularly stunning passage.

After recovering from the shock of seeing it, I became thrilled. Darwin had seen what we were alleging to be true in 1971/1972. The trade secret was real! Stasis was a Thing. It was another form of Al Gore's Inconvenient Truth!

Yet Darwin scrapped the idea as soon as he proposed it. Leaving us with something to do. Again, more on why he did that in a moment.

Years later, Bruce Lieberman (who, along with Greg Edgecombe, I am proud to say, had done their PhDs with me) and I, severally and together, worked out the gist of what a still later consortium of genetically sophisticated evolutionary biologists plus additional paleobiologists ended up concluding is the dynamics underlying species stability—the pattern of predominant non-change that has been abundantly confirmed as the common historical pattern of most species encountered in the fossil record. In other words, stasis is thoroughly established empirically as a common phenomenon in the history of life.

And widespread occurrence of species over heterogeneous landscapes leads to different local evolutionary histories of populations. Widespread species as a whole, in other words, seldom if ever evolve to adapt to environmental change. Rather, species tend to track their preferred habitats as they shift. Evolutionary adaptation is their last option.

As it happens, the 10 of us published our paper (Eldredge et al. 2005) on "The Dynamics of Evolutionary Stasis" in a supplement of *Paleobiology* dedicated to the memory of Steve Gould, edited by Elisabeth Vrba and myself in 2005. It was a rather long time interval between 1971/1972 and 2005, but it took the passage of time to find a quorum of evolutionary geneticists with minds sufficiently open who were able and willing to concede even the possibility that stasis is the pattern shown by most species most of the



Figure 1. Steve Gould, Norman Newell, and Niles Eldredge (left to right) celebrating Norman's 90th birthday, in February 1999 at the American Museum of Natural History. Courtesy of Gillian Newell. Used by permission.

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time. John Thompson, himself dedicated to understanding the relentless evolutionarily internal froth and turmoil of genetic change, and I wondered how our two very different views of life could be reconciled. The answer was, of course, the phenotype and genotype operate at different levels. Mutation and selection are each different in the quasi-isolated small populations that comprise typical species—as they are spread out over nontrivial expanses of terrain. There can be no expectation of either normalizing or directional selection acting on an entire species throughout its geographic range. The differential histories of geographically disjunct populations within a species will most likely cancel each other out through time.

So one thing we achieved in those papers in the early 1970s was the acknowledgment of the reality of stasis. And that stasis, rather than constituting a threat to evolutionary thinking, emerges as a fundamental phenomenon that needs to be explained in evolutionary terms.

And, to save the day, we saw the importance of geography in evolution—specifically the commonness of allopatric speciation as developed the generation before us, predominantly by Theodosius Dobzhansky (1937) and Ernst Mayr (1942). We simply co-opted that theory and applied it to our own paleontological data.

And, I should add, we were inspired as well by the work of the paleontological component of that New York triad of Dobzhansky, Mayr, and Simpson. Simpson's (1944) "quantum evolution" taught us that patterns of morphological change in the fossil record could and should be taken seriously—that is, they are not invariably the artifact of poor preservation. Simpson's quantum evolution, applied mostly to the evolutionary origins of higher taxa, also theoretically embraced the origins of species—though he mentioned that only in passing and without recognizing the prevalence of species-level stasis.

But, in 1972, in version 1.1 of "punk eek" (i.e., the first being the "Allopatric Model" paper I published a year earlier, in 1971), we did propose an additional component. We saw species as spatiotemporally bounded entities, with births (speciation), histories (mostly static), and deaths (extinctions)—even if we did not put it in exactly these words at that point. That paved the way for seeing the differential survival of species (with Vrba adding differential births as well in 1980). Steve Stanley's (1975) "species selection" helped clarify the vision that evolution operates at different levels.

And that, in turn, has led to a lot of work, including hierarchy theory that I pursued with Stan Salthe, Marjorie Grene, Elisabeth Vrba, and others starting in the 1980s. Among other things, exploring how the world of matter/energy transfer (ecology or economics) interfaces with the genealogical, more-making world of information storage and transfer, plus patterns of stasis and change. A dual-hierarchy scheme that came out of the punk eek–inspired contemplation of the ontology—the fundamental nature—of species. And thus other entities—like ecosystems.

Most recently, I have been collaborating with Andrej Spiridonov, who has taken the dual hierarchy scheme and enriched it with his vision of an "in-between" hierarchy of entities that fuse the elements of the largely separate ecological and genealogical hierarchies. This "Bretskyan hierarchy" (Eldredge 1985) is the eco-genealogical equivalent of the Linnaean hierarchy—embracing at its fullest extent all systems of life, from the simplest organisms up through the largest regional biomes—culminating in Gaia. Gaian biomass spatiotemporally is equal to the biomass of the Linnaean hierarchy: Nature's dual way of dividing up life (Spiridonov and Eldredge 2024).

And here I must acknowledge, back in the day, Steve Gould's rejection of the ecological side of life's ledger. In what really must be submitted as a candidate if the *Guinness Book of Records* ever includes an entry for "the world's longest footnote," in his monumental final book *The Structure of Evolutionary Theory* (2002: p. 642), Steve rejects inclusion of the ecological hierarchy, basically because it makes things too complicated. He says it is the only major point we ever disagreed on—which I think is true. I include this here if for no other reason than to say that Steve and I loved to argue with one another—and by no means did we agree on everything. But especially this very major point involving matter–energy transfer in addition to reproductive more-making in a complete characterization of evolutionary systems.

Steve signed a copy of this book to me, in his hotel room. His bed was littered with scans of the malaise that would soon kill him. We were at yet another meeting, this time back in Washington. I was speaking on the Sloshing Bucket—my attempt to flesh out the dry analytical bones of dual hierarchy (Eldredge 2003). Steve told me it was "a good speech." Amicable, and extremely sad, last meeting with a pal and partner—where argument made us seem more alive than the very useful, but more bland, agreement we had on most things. However radical.

And just recently, I am happy to say, the perspective that first propelled punctuated equilibria into becoming a full-blown hierarchical theory of biological evolution has been expanded still further into the realm of cultural entities and evolutionary processes in an important new book *The Dynamics of Cultural Evolution* by archeologist Michael Rosenberg (2022).

We geologists tend, naturally enough, to look at the outside, physical, thus abiotic world, with its own processes of energy flow and state changes, as setting the basic and boundary conditions of Life itself: how life began, and how life has survived, both unchanged and changed, for billions of years. We do acknowledge biotic interactions as causal vectors as well—but speaking personally, it is the physical world that determines, ultimately, most of the major events in the history of life.

In the late 1980s, after nearly a decade of the Alvarez impact on our collective thinking about the nature and causes of mass extinctions, a punk eek–derived epiphany bearing very closely on the origins, histories, and extinctions of species was coming into view. Norman Newell, our original mentor, had been the virtual lone voice in the wilderness in acknowledging the very existence and importance of mass extinctions—which he called "crises in the history of life." Steve and I and the rest of us during the 1960s were well-imbued with these cross-genealogical snuffing-out events—some so devastating that species of all larger taxa, on land and sea, had been directly affected. So much so that, after one particular seminar, Steve muttered to his fellow classmates (in the graduate student bullpen), "I swear that man will be going to his grave retracting natural selection"—so constant was the focus on extinction rather than on what we thought was the more interesting part of life's history: evolution. As if Newell focused on failure rather than success. The penny hadn't yet fully dropped that there is no appreciative morphological evolutionary change without the prior cleansing effects of a proper, good-old mass extinction event. As Ian Tattersall's father Alfred once remarked to his son: "Where there is death, there is hope!" Said in a different context, of course, but easily a motto that applies to the entire history of life, in my opinion.

One day in the late 1980s I met up with Carl Brett in a Burger King in Hamilton, New York—gaining coffee and caloric sustenance before a much looked forward to day in the field. At one point, Carl looked at me and said something like: "Niles, it's not just your trilobites. Nearly every other element of the

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Hamilton fauna is the same: there at the beginning, stable throughout, gone with the rest of them in what proves to be the end." Something to that effect. Carl had been developing his ideas on coordinated stasis and the Hamilton Group biota was an especially clear example (see, e.g., Brett and Baird 1995). I had seen that, but lacked the data on brachiopods, etc., to be confident to make such statements publicly. Carl was certain it was so.

Around the same time, Elisabeth Vrba was thinking along essentially similar lines. Just on the verge of moving full-time to Yale, she published a paper in the essentially U.S.-embargoed (still is!) *South African Journal of Science* (Vrba 1985) that was unexpected, certainly by me, and I assume Steve and others familiar with her earlier work. Steve and I had worked with Elisabeth and had been aware of her thinking since 1980—where it was used as the sole illustrative component of Roger Lewin's account (in *Science*) of the 1980 Macroevolution Conference at the Field Museum in Chicago—a meeting generally understood to be a referendum on punctuated equilibria (Lewin 1980). Her 1980 paper was carefully thought through, based in largest measure on her empirical work on the phylogenetics of two sister clades of African antelope.

Punk eek in action, but in her 1985 "Environment and Evolution: Alternative Causes of the Temporal Distribution of Evolutionary Events," Elisabeth dramatically expanded things: this was the first appearance of her "turnover pulse hypothesis": a distillation of a common pattern of physically driven (i.e., climatic) regional biotic disturbance and species-level extinction, with succeeding biotas a reflection of survival of some older taxa and some new taxa invading and taking up residence in the new environments. And the evolution of new taxa. In her Ur example, the environmental change was the fragmentation of wet woodlands and the development and spread of grasslands in eastern and southern Africa.

What I hadn't grasped at first, though, is Vrba saw habitat fragmentation and replacement as not only a driver of extinction, but also the driver of speciation events. A sort of micro-allopatry—where the resultant paleontological pattern would show little or no stratigraphic overlap between putative ancestors and their putative descendants. Originally, Steve and I both saw that, to be a convincing example of punk eek, there had to be demonstrable stratigraphic overlap between ancestor and descendant. And, originally, it is almost like we saw the process of speciation and replacement in the fossil record as occurring in an ecological vacuum. What Elisabeth and Carl, separately, had shown is that when these patterns occur, entire regional biotas are involved.

So most morphological evolutionary change is concentrated in speciation events involving entire biotas triggered by environmental disturbances that simultaneously drive many preexisting taxa extinct. That is the picture that emerged—and the one that still rings of profound truth in my mind. It is an outgrowth of seeing the inherent stability of species through time. And it is all empirically based: both stasis and the extinction/diversification events.

The complete spectrum of empirical levels of the effects of physical disturbance on biological systems ranges between localized catastrophes and wipeouts, up through the species level—and on up into global events and effects of the extinction and subsequent rebound evolution of higher taxa. But species are the fulcrum: these mate-recognition systems that are ± discrete packages of genetic information, with their origins, stable histories, and inevitable ends. Once gone they do not come back. They cannot—though ecologically similar species of course may well evolve. Once gone, they are lost—despite the fantasies of some dinosaur-loving kids who grow up to become molecular biologists instead of paleontologists.

And, once again, this is something that Darwin caught a glimpse of. In his 1844 *Essay* (Darwin 1844)—in his last coherent statement of evolution before he began to write his "Big Species Book" in the mid-1850s, soon to be abstracted in a Wallace-driven rush to a short paper and *On the Origin of Species by Means of Natural Selection* (Darwin 1859)—Darwin scribbled a footnote, a *pithy*, *short* footnote that his son Francis discovered and published in a footnote of his own (Darwin 1909: p. 145n2): "Better begin with this. If species, really, created in showers over world, my theory false." Darwin had just received and read his nemesis Alcide d'Orbigny's 1842 *Paléontologie française*, in which d'Orbigny introduced and paleontologically characterized his term "étages" (which is of course the same word as our "stages"). D'Orbigny preceded Darwin in South America. They corresponded over fossil shells and other things after they were both back. D'Orbigny seemed to live rent-free in Darwin's head—as he wrote letters home from the *Beagle* to his cousin Fox worrying that d'Orbigny was finding most of the goodies. And now, in addition to *Paléontologie française*, d'Orbigny was beginning to issue beautifully illustrated monographs of the Recent fauna of South America. I believe it possible that the four volumes on fossil and Recent barnacles that Darwin went on to produce were inspired in large measure by the monographs his French rival was beginning to publish.

But while d'Orbigny may have been the superior field naturalist, it was Darwin, of course, who came home with theories of mountain building, coral atoll formation, and biological evolution. And his barnacle monographs are impressive in their own right.

But—back to the question raised earlier—just why did Darwin abandon geographic isolation/speciation in favor of the alternative simple passage of geological time as the main causal impetus for morphological change and the appearance of new species? Late in his life, Darwin wrote in 1878 to C. G. Semper, admitting his long-standing vacillation over the relative importance of geography versus time in evolution: "I remember well long ago oscillating much: when I thought of the Fauna and Flora of the Galápagos Isld, I was all for isolation,—when I thought of S. America I doubted much" (quoted in DaSilva et al., in prep.).

In the first edition of *Journal of Researches* (aka *Voyage of the Beagle*) (Darwin, 1839: p. 399), Darwin says that the biota on the eastern and western flanks of the Andes are appreciably different. In yet ANOTHER footnote, he remarks that if we didn't agree with Mr. Lyell on the "immutability of species," the differences "might be considered as superinduced by different circumstances in the two regions during a length of time" —a comment often seen as an early public hint that Darwin had been thinking about evolution throughout the 1830s, if not before. But, metaphorically gazing eastward from the Andes, and conjuring the vast expanses of pampas and more southerly Patagonian scrubland plains, Darwin could see no geographic barriers (save the Banda Oriental near the Atlantic coast) that might serve as a separator for faunas to have at least partially separate histories.

In other words, Darwin needed physical isolating mechanisms, and he could not see them over the vast stretches of the lower half of South America. He wanted a general theory—and there are more species on continents than there are on the smaller islands, even island chains, bordering the continental surface. But the problem did nag him: he knew, and remarks upon it in that same 1839 volume, that there are at least four distinct living

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species of armadillo occurring over those vast southerly reaches—and that as many as three could be found sympatrically.

There was diversity that could not be totally ignored—and so when Darwin returned to recording notes on evolutionary matters in the 1850s, he framed his principle of divergence. It was to become almost the sole focus of the one diagram—that large foldout depicting hypothetical phylogenies and evolutionary patterns. His principle of divergence, in its several versions (I have counted four discrete instances in his text in the *Origin*) are entirely biotic: basically, descendant varieties, arising parapatrically but without full geographic isolation, are more specialized, and either outcompete the parental species or occupy different "niches" to become fully separate, full-fledged species. To my knowledge, this part of Darwin's argument has failed to gain much if any traction in the minds of his intellectual descendants.

The problem was simply that an understanding of the nature of climate change was in its infancy. Louis Agassiz (who later became an ardent opponent of Darwin's evolutionary ideas) had his earliest publications on glaciers in the 1830s. In short, no one saw what Elisabeth Vrba so clearly saw and so strongly stated in 1985: global climate change can lead to habitat fragmentation and alteration, which in turn leads to extinction, as well as to species fragmentation and therefore speciation.

Four-dimensional patterns in evolutionary time. Especially clearly seen because species are spatiotemporally bounded entities, with origins, more or less stable histories, and eventual and inevitable deaths.

The foundational empirical ontological basis of punctuated equilibria.

I have come to see—as a result of such analysis and the growth and additions by the evolutionary, biological, and paleobiological communities at large—the importance of detailing the ontological nature of biological entities. There are two great classes of biological structure and function: economic, matter and energy transfer actions; and reproduction. More making of entities of like kind.

And so I have come to prefer this definition of evolution: the fate of transmissible information in an economic context. Evolutionary patterns of stasis and change occur within the realm of sexually reproducing organisms. Also asexually reproducing systems. Not only bacteria—but cells within the somas of sexually reproducing individual organisms. Think of immune systems. Cancer. Even (possibly) the brain. And sociocultural systems as well. Not only material cultural evolution, but languages—and larger-scale entities such as social institutions and social organizations, such as communities and nation-states. Culture in general.

All valid domains of evolution, insofar as I can see. All currently under study. And in all the publications, we invariably find the language of punctuated equilibria echoed as patterns are recognized—and causes mooted and argued over. Stasis; punctuation; gradualism; selection; and sorting among higher level entities. And so on.

This continues to be fun!

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