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The **THIRD CULTURE**



by John Brockman

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NILES ELDREDGE: Punctuated equilibria rests on a basic empirical claim, which is that once a species appears it typically doesn't change very much. If you're talking about marine invertebrates, that means five or ten million years. Yet evolution does, of course, occur, and the change seems to be associated with speciation events, in a formal sense. There's no intuitive reason why that should be true, because speciation is the setting up of new reproductive communities. It shouldn't have anything to do with adaptive change whatsoever, and yet it seems to.

I'm known for my work, in association with Steve Gould, on punctuated equilibria, also on fleshing out the hierarchical structure of biological systems: the ecological and genealogical twin hierarchies. It's basic ontology. Punctuated equilibria was a matter of putting Theodosius Dobzhansky's and Ernst Mayr's attention to the nature of species and discontinuities between them arising from the process of speciation, together with George Simpson's attention to evolutionary pattern in the fossil record. The resulting implications—one of which is the nature in general of large-scale biological systems—have occupied most of my attention.

There are several important paradoxes raised by the very notion of punctuated equilibria. One has to do with long-term evolutionary trends. If you look at long-term events in evolution within a group, like increased brain size in humans over four or five million years, the old model is that natural selection favors bigger brains, and so over four million years you get bigger and bigger brains. If you look at the fossil record, you do get bigger and bigger brains as you go through time, but it's a stepwise pattern, not a gradual thing. The raw

statement of punctuated equilibria removed the old convenient element of directionality for long-term trends in the fossil record. But if you concede that there's a directionality over time, what is the explanation?

What we're saying is that species are entities. They have histories, they have origins, they have terminations, and they may or may not give rise to descendant species. They are individuals in the sense that human beings are individuals, albeit a very different kind of individuals. They're large-scale systems that have an element of reality to them, and that's a big departure in evolutionary biology. There are some adumbrations of it, but certainly it's not traditional. Our notion—sometimes called "species selection" or "species sorting" (a better term)—sees the differential origins and extinctions of species as an important additional element shaping the history of life, including the production of long-term evolutionary trends.

Species are real entities, spatiotemporally bounded, and they're information entities. Other kinds of entities do things. Ecological populations, for example, have niches; they function. Species don't function that way. They don't do things; they are, instead, information repositories. A species is not like an organism at all, but it's nonetheless a kind of entity that plays an important role in the evolutionary process.

This is an ontological shift. Geneticists remain underwhelmed with the notion that species are real entities, simply because they think that their data (generation-by-generation change within populations) don't demand it. So John Maynard Smith, whom I respect a great deal, won't respond to the gambit that species are real entities, with actual roles to play in the evolutionary process, simply because he doesn't personally find it interesting. Richard Dawkins is trying to force everything into a genic explanation. It's ships passing in the night. You don't need that kind of concept at all, if you're just dealing with generation by generation, running the natural-selection algorithm. I don't blame those who don't find this interesting. It's our job to make them understand that construing species in this way adds a valid and interesting element to evolutionary theory.

I call people like Steve and myself "the naturalists," in contrast with our gene-minded colleagues, the ultra-Darwinians. We try to capture the middle ground. The three main characters in the ultra-Darwinian camp would be Maynard Smith, George Williams, and

Richard Dawkins. All of us agree on the rudiments of evolutionary change: adaptive modification through natural selection. The one gloss on it that ultra-Darwinians have developed is that the fundamental dynamic underlying all of biotic nature is a competitive urge to leave copies of your genes behind. Making bits of information—genes—compete with one another makes evolutionary biology seem more like physics, so my accusing ultra-Darwinians of physics envy is probably the snottiest thing I could say about them.

Punctuated equilibria reasserts the importance of discontinuity in evolutionary discourse. Though it's usually the ultra-Darwinians who are cast in the role of *defensores fidei*, it was actually Mayr and Dobzhansky, as founders of the "modern synthesis," who originally managed to inject an element of discontinuity into the evolutionary discourse. So it's actually we naturalists who are defending a corner of orthodoxy here. As Dobzhansky said, Darwin established the validity of natural selection, and natural selection generates a spectrum of continuous variation. But nature is discontinuous. It's discontinuous (as Dobzhansky said in 1937) at the gene level and again at the species level. Most evolutionary biologists are population geneticists, and so they don't, as I just said, see the significance of intraspecific discontinuity. The data they handle aren't at the intraspecies level. They're not used to thinking about these problems, so a lot of that early discourse, hard-fought and hard-won, about the differences between species, defined as separate reproductive communities, doesn't enter into their universe. That's O.K., in a sense, because, what the hell, you talk about the stuff that impinges on your consciousness, and what your data are all about, and there's a lot to be said about the forces affecting the frequencies of genes on a generation-by-generation level within populations. But to restrict the discourse to species is to ignore other elements of biological organization, and ultra-Darwinians do so at their peril. Theirs is an incomplete description of biotic nature, rendering their theory simplistic and incomplete. It's disturbing that in his recent book *Natural Selection*, George Williams goes out of his way to stress that species are no special category of biological entity.

Ultra-Darwinians generally deny that they're genetic reductionists, but by anyone's definition they absolutely are. They try to explain the structure and history of large-scale systems purely in terms of relative gene frequencies. Social systems, economic systems,

ecosystems, and so forth, all flow from this supposed competition among organisms—or even worse, among the genes. So what they're doing is actually playing fast and loose with a lot of work that's been done over the last fifty years establishing the actual nature of large-scale biological systems like species, like ecosystems—like social systems, for that matter—because they have a very gene-slanted view.

In a sense, I think it's intellectually incomplete, rather than dishonest. I always feel that if you're going to critique somebody you ought to know how to sing their song, and I feel like I spend a lot of time learning how to sing these guys' song. I don't see them turning around and learning the song that Steve and I and Elisabeth Vrba and Steven Stanley have been singing. I think they're so wrapped up in their own gene-centered world that they have an incomplete ontology of biological nature.

George Williams was the one who began taking evolution out of the passive mode and making it active. The translation of this is that organisms are out there competing, and although it looks like they're competing for food, they're competing for the opportunity to leave more genes behind. At the reproductive-biology level, it's a good description of nature. As a rubric to explain what's going on in biological nature in general, especially in large-scale biological systems, it falters—increasingly as you enter larger-scale systems and particularly as you address economic rather than reproductive phenomena.

Dawkins says in *The Selfish Gene* that ultimately we'll be able to understand the entire internal workings of ecosystems—the rules of assembly and what keeps them together—based on this particular principle of genic competition. It's an appeal to reductive thinking, and an attempt to turn into an active principle what Darwin was content to leave as a passive principle.

This is a subtle point. Ultra-Darwinians are reductionists, but only down to the genes-within-populations level. They're afraid of still lower levels: most population geneticists freak out when they hear a molecular biologist like Gabriel Dover talk about evolution! What we're saying is that there are more levels, both higher and lower, than in the traditional bailiwick of population genetics. Things are a little more complex, and we can specify to some degree what that complexity is.

If you read Dawkins' *The Blind Watchmaker*, it presents a seemingly adequate theory of why organisms appear to fit their environ-

ment so well—in other words, how natural selection shapes organic adaptation. But on closer scrutiny, you find that there's absolutely nothing in there about why adaptive change occurs in evolution. There's really nothing about the context of adaptive change. It's just not addressed; it's not even an issue. It's just an in-principle argument. The algorithm is described in loving detail, and the supposition is that you just let the motor run and all the stuff we see—all that three-and-a-half-million-year history, those ten-million-odd species we have on Earth right now—simply falls out of that. The rest of it is mere detail. The important thing is to get the mechanism.

As I've said, we all basically agree on the statement of the mechanism, which Darwin established. Nobody's going to argue against it. Trying to make Steve Gould out as an anti-adaptationist is crap. Maynard Smith had a symposium in 1978, and as he himself says, the most visible thing that came out of it was the paper Steve wrote with Dick Lewontin called "The Spandrels of San Marco and the Panglossian Paradigm," saying that there's this adaptationist program and its proponents assume that every biological structure we look at was carefully chosen by natural selection. It's just an assumption, and hard to show rigorously, and there are an awful lot of other possibilities. That statement cast him in the role of being an anti-adaptationist.

The adaptationism of Maynard Smith, Williams, and Dawkins can be explained as follows: there's design in nature, organisms look like they're fairly well suited to the environment they find themselves in, and they're functioning pretty well out there. The only explanation for this state of affairs that makes any sense, other than the notion that a creator did it, is the process of evolution—particularly through natural selection, where the best-suited variants in the population tend, on average, to leave more copies of their genes behind than others less well endowed. Over a process of generations, nature will cull out and push things, giving the requisite variations. Those are the ground rules; everybody accepts that. What we naturalists are saying, in contrast, is that natural selection seems to produce adaptive change mainly in conjunction with true speciation—the sundering of an ancestral reproductive community ("species") into two or more descendant species.

A lot of the debate between Dawkins and Gould is trying to show each other who's brighter and more clever. I sometimes think they're

almost deliberately misconstruing each other. It's a battle of words, a battle of wills to try to inform the literate public about who has the *best* approach to nature.

Steve has always been ready, willing, and able to jump in there and joust with the Dawkinsses and Maynard Smiths of this world. It's taken me a longer time to get to that point. I focused first on reconciling patterns of stasis and change in the fossil record with the views of my immediate predecessors—Simpson the paleontologist, of course, but also Mayr the systematist, and even, oddly, Dobzhansky the consummate naturalist-turned-geneticist. I had to get past seeing Simpson, Mayr, and Dobzhansky in the Oedipal sense—as father figures whose work I had to correct. I had to come to understand that the punctuated-equilibria idea actually reconciles some serious discrepancies between Simpson, on the one hand, and Mayr and Dobzhansky on the other. Once done, the radical implications of punctuated equilibria stood out in bolder relief, and I could turn my attention more fully to the modern ultra-Darwinians. It's only now that I'm ready to take on people like Richard Dawkins and Maynard Smith and George Williams.

George Williams makes an interesting, if depressing, observation in *Natural Selection*. He says that a lot of the problems aren't so much solved as that people stop probing them and convince each other that they're solved well enough. We don't so much solve scientific problems as abandon them. That's kind of chilling, but it's a good description of what goes on. What I'm saying here is that there's no final resolution to the current debates. The millennial issues of human overpopulation, large-scale environmental destruction, and species loss probably will—probably should—distract us from the less pressing concerns of pure evolutionary theory. The issues will be picked up again someday, but by our intellectual descendants.

STEPHEN JAY GOULD: Niles Eldredge is my closest and dearest colleague in science. Whenever two people are so strongly connected, as we have been through punctuated equilibrium, people inevitably try to drive wedges, and yet although some attempts have been made no one has ever succeeded.

I receive more attacks, and people are often attacking other things that I stand for, because I have a more public reputation. But Niles and I don't agree on everything by any means. For example,