Stephen Jay Gould was a force of nature. A perusal of Google metrics indicates he was the most read and cited evolutionary biologist ever, well more than Charles Darwin himself, and more than five times than Ernst Mayr. Gould reached the lay public like no one ever has. Since his passing in May 2002, several volumes have tried to bring a measure of order to Gould the person and to his voluminous writings on paleontology, evolution and a myriad other topics, what they have meant and accomplished, and his quest for a unified, modern evolutionary theory (Eldredge and Vrba 2005; Allmon and others 2009).

Gould's forte was not empirical biology and paleontology. Rather, it was his ability to see conceptual connections across disciplines, and it was his ability to think and write about those connections. As Tattersall notes in the volume reviewed here, “But Steve himself was never a detail man, certainly as concerned anthropology. His great strength always lay in the big picture” (page 125). This explains why there are more citations of his popular work than of his scientific work (about 20% of his 814 publications were peer-reviewed; Allmon 2009:335), but extraordinarily, the reach of both is far, wide, and deep. In short, there has ever been anyone like him … even if one thinks back to other icons who also had their feet in both these camps (Thomas H Huxley, Richard Dawkins, and Carl Sagan spring immediately to mind).

Stephen J Gould: The Scientific Legacy emerged from a 2012 meeting at the Istituto Veneto in Italy to explore Gould's success in forging an understanding of the structure of evolutionary theory as well as his legacy in, and impact on, fields as diverse as evolutionary developmental biology, anthropology, and economics. Although no single book can capture all this (see also Eldredge and Vrba 2005; Allmon and others 2009), the thirteen chapters are largely great reads and insightful about Gould's contributions; a few only tangentially weave Gould's thoughts into their narrative and are therefore somewhat less successful. As a whole, the volume admirably summarizes many of his contributions in setting new conceptual agendas and shifting fields as diverse as paleontology, evo-devo (evolutionary developmental biology), paleoanthropology and human evolution, and the role of hierarchy theory in evolution. These chapters are not meant to be deep critical analyses of Gould's work, although authors do occasionally acknowledge differences with him.

The lead chapter by Niles Eldredge, aside from addressing the background and writing of his and Gould's seminal “punctuated equilibria” paper (Eldredge and Gould 1972), recounts Gould's early days at Columbia University. I was also there at the time and can attest that it was a very heady environment for any young student in evolutionary biology. The place was crawling with vertebrate and invertebrate paleontology students in the Geology
Department but there were also some of us over in Zoology as well. We all participated in the four paleontology classes taught at the American Museum of Natural History, which also was populated with multiple postdocs and researchers. We could also avail ourselves of Theodosius Dobzhansky's population genetics seminars at Rockefeller University. It was an amazing time, and as Eldredge describes so well, Gould was clearly a leader, which was driven home by his sophisticated PhD seminar talk before he rushed off to Harvard. Moreover, this chapter is a must-read if you want to get the inside view on the intellectual environment surrounding the punctuated equilibria revolution.

It is not possible in this space to discuss all the chapters in this book, but a number of them illustrate the breadth of Gould's influence and are thus worthy of brief attention. One of the first chapters, by the philosopher of science Elisabeth Lloyd, revisits the famous “spandrels of San Marco” paper by Gould and his Harvard colleague Richard Lewontin (1979), in which they provide a counterpoint to the prevalent Darwinian adaptationist explanation for functional traits. They argued that there may be multiple explanations for a trait other than adaptation per se. Lloyd herself makes a case for the potential nonadaptive origin of traits based on her extensive analyses of the evolution of female orgasm. She thinks that the take-home message of the spandrels paper is seen as passé within evolutionary biology: “Evolutionists all say that they have learned their lessons about an inclusive approach to evolutionary explanation from Gould and Lewontin's 1979 spandrels article, but methodological adaptationism [that is, assuming at the outset that an adaptationist argument is likely correct] seems to make it very difficult for them to act on those lessons” (page 34). She supports investigating multiple kinds of explanations: recognizing that adaptation is usually a viable first choice, she warns that hidden assumptions about your first choice come with risks not always realized.

If we see the phenome, the sum of all phenotypic traits, as something more than simply traits that can be scored in specimens, as something also encompassing structural variation all the way down to DNA, then it seems clear there will be few simple general explanations—adaptationist or otherwise—to account for all the phenotypic variability. T Ryan Gregory looks at these issues at the genome level, guided by many of the themes that Gould discussed time and time again. We still have scant understanding of intragenomic selection, as well as fitness effects at the cellular or organismal levels, so traditional adaptationist explanations placing fitness effects at the organismal level might not work. Moreover, Gregory suggests that taking a hierarchical view of evolutionary processes, instead of assuming that selection is only operating on changes in coding regions, will be essential for explaining the new data of comparative genomics.

Alessandro Minelli does a thoughtful job of laying out and analyzing ideas about hierarchy and levels of selection. He shows how this new thinking, led by Gould and others, counters the standard view of Darwin and then later, the “modern synthesis.” He notes that concepts about individuality (underlying the idea of punctuated equilibria), the distinction between interaction versus inheritance when talking about the units and locus of selection, and the notion of hierarchical patterns of evolutionary processes are deeply important. He rightfully laments, “The apparent silence of professionals on these aspects of evolutionary theory to which Stephen Jay Gould devoted a large part of his immensely productive career must not be construed as a proof that he spent so much time and effort on questions of marginal relevance” (page 81).
Another chapter that bridges many of Gould’s ideas—as expressed in his book *Ontogeny and Phylogeny* (1977), as well as in multiple papers including the “spandrels” paper—and brings them forward into the modern world is Gerd Müller’s discussion about the conceptual foundations and history of evo-devo. He argues that this dynamic field, in many ways initiated due to Gould’s influence, is requiring new ways of thinking about natural selection and adaptation, indeed about the entire structure of evolutionary theory itself. Although the chapter is written by a major player in this discipline who has a stake in the game, it makes numerous important points about a new “extended synthesis” involving evo-devo that need to be taken seriously. Here, too, is another chapter that argues that Gould’s ideas have been ignored by many evolutionary biologists.

The third part of the book includes four chapters devoted to Gould’s intellectual legacy in anthropology. Two of these directly link Gould’s writings with changes in the field. First, Ian Tattersall argues that Gould’s contributions to paleoanthropology were “truly seminal.” And when you tally up Gould’s writings about ontogeny and human evolution, on the theme that human evolution (seen as anagenetic and transformational) was not a ladder but a bush/tree with many branches (species), on brain size versus intelligence, and on scientific racism and the foundations of intelligence, it is indisputable that his influence was profound. Gould did not always come out on the right end of things, but he changed the dialogue within a discipline that was not his own.

Guido Barbujani brings Gould’s book *The Mismeasure of Man* (1981) into the genomics era. Whether human populations can be apportioned into races, or kinds, or evolutionary groupings that reflect human history rather than human mismeasure or prejudice has occupied anthropology since humans became fodder for study. Barbujani expertly summarizes all these missteps. But in an era of genome sequencing, human history is being turned upside down. We can now trace lineages and migrations across the globe and we can estimate when people first occupied different geographic regions. We can also trace the intermingling of our ancestors, the most spectacular one perhaps being Neanderthal introgression. Genomic analysis is also revealing that human differences are much smaller than expected given the phenotypic diversity we see. Barbujani puts forward a thoughtful discussion about the intersection of genomic data on variation, human disease, and the continued use of racial categories within the medical community. He notes, “Contrary to the claim that racial stereotypes capture some meaningful aspects of biological variation, the available data indicate that to predict whether an individual will have certain health risks or will benefit from pharmaceutical treatment, one must study that individual’s genes” (page 142). Nevertheless, he is a realist:

It is hard to see how the race concept can still be regarded as a useful tool for addressing these and similar questions. However, race does remain an important component of our social and psychological world. This component affects human interactions and social policies, and will not vanish just because some scientists say it has no objective basis. In a sense, then, races exist, and should be kept into consideration. However, on the basis of what is known, they exist only in the sense that the labels we stick on ourselves and on the others have practical consequences, even if they do not correspond to empirically identifiable biological realities.... (page 143)
The editors and authors are to be congratulated for capturing much of the breadth of Gould’s influence. Personally it brought many memories to the surface. I knew Steve as a fellow student and classmate, and very early in our scientific careers as roommates at a NATO Advanced Study Institute on vertebrate evolution in Istanbul in 1969. We saw and interacted with each other many times over the years. No encounter was perhaps more important than the time I was privileged to be in his and Niles Eldredge’s hotel room and to read the manuscript the night before Steve’s talk unleashed punctuated equilibria to the world at the Geological Society of America meeting in 1971. Reading the chapters of this book gave me a deeper appreciation of his body of work and thinking. Steve’s ideas still should give scientists much to argue about, and importantly many are still very much worth arguing about.

REFERENCES


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