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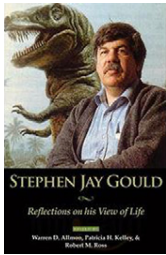
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Ever since Gould

Stephen Jay Gould: Reflections on His View of Life edited by Warren D. Allmon, Patricia Kelley and Robert Ross. Oxford University Press, 2008. £18.99, hbk (416 pages) ISBN: 978 0 19 537320 2

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By my count, Stephen Jay Gould changed the way that evolutionary biologists think three times: (i) introducing punctuated equilibrium [1]; (ii) rescuing and jump-starting the long-discredited field of evolution and development in *Ontogeny and Phylogeny* [2]; and (iii) catalyzing a debate on contingency, determinism and morphological disparity in *Wonderful Life* [3].

Gould's death in 2002 prevented his final work from changing the way we think for a fourth time. I doubt that a living Gould would have allowed two lukewarm but influential book reviews written by microevolutionists [4,5] to give evolutionary biologists 'permission' to avoid reading his admittedly long *The Structure of Evolutionary Theory* [6]. As a direct result, our field is proceeding without a widely accepted theoretical structure that appropriately circumscribes neo-darwinism as a limited and insufficient part of a larger theory.

Nowhere was Gould's life and death felt more strongly than among his fellow paleontologists. *Stephen Jay Gould: Reflections on his View of Life*, a volume of 15 essays is written by former PhD students and a few close collaborators. This book reviews the work and personality of a scientist who would make anybody's list of the top five evolutionary biologists of the second half of the 20th century. This is the second major tribute to Gould, the first being a collection of 14 significant scholarly works in a volume of *Paleobiology* [7]. *Reflections* (which includes Allmon's complete bibliography of Gould's work) undertakes a deliberately personal review of Gould as a human being and scientist, underscored by the consistent reference to him as 'Steve' throughout the volume.

The lead manuscript is Allmon's 'The Structure of Gould', a remarkably ambitious and complete attempt to intertwine Gould's intellectual and personal biography with assessments of the impact of his work on the field of paleontology. Allmon brings fresh biographical detail to the circumstances surrounding major events such as the birth of punctuated equilibrium. He also sketches the breadth of Gould's larger-than-life scope of influence and interests in society, reminding us of details such as his concern over the practice of propagating error when textbook authors copy from one another. Allmon introduces every subject taken up by the other contributors to *Reflections*. For example, his discussion of Gould's battle with creationism is followed up by Kelley's thoughtful piece on

the successes and failures of Gould's attempt to redirect this argument with his concept of non-overlapping magisteria. Allmon's discussion of Gould as an educator is followed up by Ross' fascinating contribution that chronicles Gould's fall in popularity as an undergraduate lecturer at Harvard as his accelerating tendency to digress interacted with a steep decline in student attention span.

Although it includes serious works of scholarship, the personal angle taken by *Reflections* enabled informal and often delightful personal recollections and commentary from contributors as broad as a 'hard rock' geologist who TA'd for Gould (Schneiderman) to the intellectual giants who produced the must-read gem 'What does it mean to be a radical' (Lewontin and Levins). The volume intersperses such short pieces with comprehensive reviews of Gould's intellectual impact on assigned topics, including genetics and development (Dorit) and punctuated equilibrium (Lieberman).

In my favorite chapter, Bambach reviews Gould's empirical and theoretical contributions to paleontology in some of the clearest prose I have encountered in some time. As Phil Gingrich pointed out to me, 'We [paleontologists] are the ones that can directly observe the sweep of evolutionary history'. I was especially impressed by the temporal and spatial detail that Gould was able to discover in the fine-scale study of speciation in Bermudian land snails. He was able to identify multiple abortive origins of pedomorphic types, but that these predictably arose in the same kind of soil. I am truly humbled when I contrast this resolution to the arm-waving inferences that neontologists, such as myself, make about the probable mode and location of speciation events.

I was struck by Allmon, Morris and Ivany's thought-provoking investigation of the impact on Gould's work of his personal opinion that ecology had little to offer to macroevolution. I have often asked the opposite: would ecologists more actively incorporate evolutionary biology into their thinking if they were broadly exposed to macroevolution? The strong impression left by undergraduate evolution courses is that selection is constantly and rapidly moving morphologies around as conditions change. Instead, the world that ecologists encounter daily is one in which species are remarkably static wherever they are found across their range, under a variety of conditions. In fact, the best explanation I have seen for a mechanism underlying stasis is not Futuyma's [8] 'ratchet' idea that Gould himself champions, but a source-sink argument advanced by ecologists for conservatism of fundamental niches at the edges of geographical ranges [9].

The failure of *The Structure of Evolutionary Theory* [6] to make an impact casts a pall over most of the works in this volume. Although most biologists will agree that the directionality of mutation is not random, few recognize that this means that they must re-think what it means to be a darwinist. You will enjoy *Reflections*, but please read Part I of *Structure*. Require it of your students. Skip through the sections of Part II that do not interest you, but I assure you that much of it will.

For Gould to make a lasting impact, his ideas must resonate in fields to which he paid little attention, which they do. For example, the great discovery of phylogeography has been the prevalence of cryptic species (often thousands to millions of years old) in most multicellular lineages (four cryptic species to every named species by one early count in vertebrates [10]). What are morphologically indistinguishable cryptic species but living, experimentally tractable cases of stasis whose relative frequency *vis à vis* morphological change can be assessed? In fact, the most consistent theme of *Structure* is the future of evolutionary biology, in that we must develop unbiased researched programs to evaluate the relative frequency of evolutionary processes. To achieve unbiased estimates, Gould proposes comprehensive studies of entire monophyletic groups, or all species in circumscribed biogeographic

areas. This will indeed require big science, and to carry this off we must think not only ambitiously, but also creatively, as Gould has shown us how.

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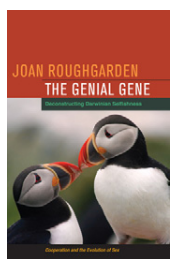
Book Review

Pitting the boys against the girls

The Genial Gene: Deconstructing Darwinian Selfishness by Joan Roughgarden. University of California Press, 2009. US\$24.95, £14.95 hbk (272 pages) ISBN: 9 780 520 25826 6

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Mandatory reading in the subject of my first education (anarchist theory) is *Mutual Aid: A Factor of Evolution*, in which Petr Kropotkin asks ‘Who are the fittest: those who are continually at war with each other, or those who support one another?’ and concludes that ‘Sociability is as much a law of nature as mutual struggle’ [1]. Kropotkin saw himself as following Darwin’s lead when the latter

wrote (in *The Descent of Man, and Selection in Relation to Sex*) that ‘those communities which included the greatest number of the most sympathetic members would flourish best, and rear the greatest number of offspring’ [2]. The comrade/lab-mates of my second education (animal behavior) remained unconvinced: ‘Really? How does this work Pete, group selection?’ Over a century later, Joan Roughgarden’s *The Genial Gene: Deconstructing Darwinian Selfishness* argues essentially the same point as Kropotkin, but with Darwin, and sexual selection (Supplementary Information §1), cast as the villains.

Similar to that of Kropotkin, Roughgarden’s controversial work is ideologically driven (Supplementary Information §2). She believes that publicly disproving sexual selection, and its proponents, is necessary for social justice to be achieved (Supplementary Information §3). In *The Genial Gene*, Roughgarden presents the ‘social selection’ theory first advanced in her Science paper [3] as a retort to Dawkin’s *The Selfish Gene* [4]. Her ‘selfish gene’ signifies an organism that is blindingly selfish. For example, she argues that birds building a nest together is contrary to ‘selfish gene’ theorising because success is not due to the selfish acts of a single individual (Supplementary Information §4). No hints in this book that ‘selfish gene’ might mean anything but this; no talk of gene-centric thinking or extended phenotypes here.

Roughgarden: ‘No one has yet figured out a useful way to decompose team achievements into individual contributions.’ However, I would disagree and suggest that game theory achieves this aim. The Stag Hunt game has long served as a model for the evolution of cooperation [5], and models shared nest building nicely. Most of *The Genial Gene* reworks elements of game theory, often very oddly (Supplementary Information §5), into the ‘Social Selection’

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