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REVIEW ESSAY

Evolutionary chance and contingency: in search for systematics

Grant Ramsey and Charles H. Pence (eds.): Chance in evolution. Chicago: The University of Chicago Press, 2016, 384 pp, $45.00, £31.50 PB

Jeroen Hopster[1,2]

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Although Darwin has been celebrated for uncovering the role of chance in evolution, he was no chance aficionado. Darwin did not like the term; echoing the intellectual consensus of the seventeenth and eighteenth century, he often relegated chance to ignorance. Over the course of Darwin's lifetime, this consensus was beginning to unravel. A great enthusiasm for using statistical methods developed, especially in the social sciences, but Darwin was not infected by it. The potential to utilize statistical methods to study evolution became apparent only later through the contributions of biometricians and population geneticists.

Nonetheless, Darwin *did* champion the role of chance in evolution, albeit in a different sense. Darwin pioneered a use of the term that would become specific to evolutionary theory: natural variations are the result of chance, in the sense that they are not occasioned by their adaptive benefits. Put differently, variations arise independently of their fitness effects. This insight can easily be connected with the view that the evolutionary process is not goal-directed, which was a revolutionary stance in Darwin's days.

That Darwin used the term 'chance' in different senses, including the just mentioned 'evolutionary' sense of chance, 'chance as ignorance', as well as 'chance as probability', is not just of historical interest, but also serves to illustrate a point about the systematics of chance: there exist different chance notions, which may be related but are not identical, and can easily be conflated. While this holds true for many fields, the use of chance in evolutionary biology is particularly rich and complex. According to one recent count, there are as many as seven senses in which evolutionary biologists appeal to chance: 'indeterministic chance,' 'chance as

✉ Jeroen Hopster
j.k.g.hopster@uu.nl

[1] Department of Philosophy and Religious Studies, Utrecht University, Janskerkhof 13, 3512 BL Utrecht, The Netherlands

[2] Harvard University, Cambridge, MA, USA

ignorance,' 'chance as not designed,' 'chance as sampling,' 'chance as coincidence,' 'evolutionary chance' and 'chance as contingency' (Millstein 2011). Other scholars may classify these uses somewhat differently or invoke even further distinctions. For example, in the volume under review, Douglas Erwin distinguishes between five different meanings of contingency. All agree that, in an evolutionary context chance has several different meanings.

This conceptual richness makes chance in evolution a topic of great intellectual interest. Whence this diversity? Are the different chance concepts related? How did they originate? To single out just one observation, note that chance is often defined *ex negativo*: in terms of something it is meant to deny or exclude (Lüthy and Palmerino 2016). For example, chance may be contrasted with 'cause,' 'design,' 'necessity' or 'purpose.' As these opposites change—and they have done so throughout history—so does the meaning of chance. This makes the concept enormously flexible, a feature that any attempt at conceptual analysis should acknowledge.

Chance in Evolution does not attempt to offer a comprehensive systematization of chance in evolution. Instead, what inspired the editors in composing this volume was the 'dizzying multiplicity of ways of understanding chance' (3). The volume contains twelve chapters that shift in several directions: some are historically oriented, whereas others focus specifically on the theoretical role of chance, as well as its conceptual cousin 'contingency.' In what follows, I pick out some of the key points made by the contributing authors, focusing specifically on those remarks that help us to come to terms with the systematics of chance and contingency.

The first part of the book is titled 'The Historical Development and Implications of Chance in Evolution.' In the chapter 'Contingency, Chance, and Randomness in Ancient, Medieval, and Modern Biology' David Depew discusses six theses regarding the concepts of contingency, chance and randomness. One of Depew's observations is that the formula 'random mutation plus natural selection,' commonly employed to characterize a Darwinian view of evolution, loosens the conceptual relation between chance and the adaptive benefits that variations might have—i.e., the specifically evolutionary sense of chance. As a result, this formula can easily give rise to misunderstandings and had better be avoided.

Jonathan Hodge's chapter, 'Chance and Chances in Darwin's Early Theorizing and in Darwinian Theory Today,' provides a thorough analysis of how Darwin's views of chance developed throughout his early writings. Hodge also assesses whether, since Darwin's days, natural selection has changed from a causal theory into a non-causal statistical theory, and concludes that it has not. He convincingly argues that there was no major shift in Darwin's view of chance before and after the late 1830s, when Darwin came up with the idea of natural selection. The 'ignorance view' remained Darwin's primary association. Intriguingly, Hodge notes that Darwin's 'determinism and ignorance view of chance allowed, indeed encouraged, Darwin to take chanciness more, not less, seriously in his theorizing, because to do so was to take seriously any lawful causation and any gaps in his knowledge of it' (50). This may seem paradoxical, but it is not without precedent: the seventeenth- and eighteen-century pioneers of probability theory (the 'doctrine of chances') were equally swayed by determinism and an 'ignorance view' of chance.

The third chapter, co-authored by Anya Plutynski, Kenneth Vernon, Lucas Matthews and Daniel Moller, discusses 'Chance in the Modern Synthesis.' The authors discern five different senses of chance that played a role in the works of the main synthesis scholars. They find some support for Stephen Jay Gould's thesis that a 'hardening' of the synthesis, i.e., progressively greater emphasis on adaptation and selection, occurred around midcentury. But they emphasize that 'there was not a philosophical or conceptual transition in the synthesis, only a change in empirical views regarding whether and to what extent drift (as a matter of fact) was an important factor in evolutionary change' (99). This chapter exemplifies how, a century after Darwin, the concept of chance in evolution has grown much richer, especially in terms of its probabilistic connotations. The 'ignorance view' has given way to a general consensus that chance can be a positive ingredient of evolutionary explanation.

In 'Is it Providential, by Chance? Christian Objections to the Role of Chance in Darwinian Evolution' Matthew Ashely recounts in much detail the arguments that the Presbyterian theologian Charles Hodge and the Roman Catholic cardinal Christoph Schönborn presented for the incompatibility of chance with Christian doctrine. This chapter is an outlier: whatever their theological interests, these Christian intramurals add little to our understanding of chance in evolution.

In 'Does Darwinian Evolution Mean We Are Here by Chance?' Michael Ruse discusses whether there is progress in evolution, focusing mostly on the views of Darwin and Gould. Although Ruse's discussion is engaging, he does not explicate what he means by chance—and given chance's many connotations, this makes his argument somewhat obscure. For example, Ruse concludes that 'few [practicing evolutionary biologists] would think the emergence of humans was entirely a matter of chance' (140-1). This could mean different things, depending on whether we understand chance in contradistinction with 'necessity,' 'progress' or 'directionality.' The context lends itself to either interpretation. As an *addendum* to Ruse's discussion, I propose to make the following distinction, which may be helpful to get a grip on Gould's position: a chancy process versus a chancy outcome. Arguably, on Gould's view, the *process* of evolution as a whole is entirely chancy, in the sense of being undirected—an argument laid out in detail in Gould (1996). However, if we focus on specific *outcomes* of the evolutionary process, such as the evolution of Homo sapiens, then various arguments may be advanced to the effect that their evolution is *not* entirely a matter of chance.

The second part of the book, 'Chance in the Processes of Evolution,' opens with a chapter by Michael Strevens: 'The Reference Class Problem in Evolutionary Biology: Distinguishing Selection from Drift.' Strevens argues that the problem of distinguishing selection from drift is akin to the reference class problem, which, in its broadest formulation, is the problem of determining what factors should be taken into account in determining the probability of an outcome. Call the factors that are taken into account 'parameters' and the factors that are not taken into account 'variables.' The reference class problem, then, is 'the problem of deciding whether a causal factor is to be treated as a variable or a parameter' (146). Strevens' discussion of this distinction as applied to selection versus drift is fairly technical and will be of interest mostly to philosophers of science.

By contrast, Francesca Merlin's chapter 'Weak Randomness at the Origin of Biological Variation: The Case of Genetic Mutations' will be of interest to a broad audience of philosophers and biologists. Merlin distinguishes 'weakly random' from 'strongly random' events and argues that, from an empirical point of view, all genetic mutations at the molecular level are best characterized as 'weakly random.' Merlin characterizes a 'strongly random' event as an event that results from (i) an indiscriminate sampling process and (ii) is invariant over time. A 'weakly random' event is the result of a stochastic process that does not fulfill both of these conditions [(i), (ii) above] at once. Research from the past two decades has shown that there are various biases that affect the process of mutation, such that these conditions are not fulfilled. Hence, models that portray mutations as 'strongly random' are idealized and should be refined.

The chapter by Thomas Lenormand, Luis-Miguel Chevin and Thomas Bataillon, 'Parallel Evolution: What Does It (Not) Tell Us and Why Is It (Still) Interesting?' discusses two different views of parallel evolution: the view of 'selectionists' and that of 'mutationists.' Selectionists stress that parallelism is the result of adaptive solutions to common problems, whereas mutationists stress that parallelism is the result of mutational constraints. The authors point out that it is often difficult to decide whether parallel evolution is the result of adaptation or of mutational constraint—an important point, although not an original one. Evolutionary constraints are also of key importance in the debate over the contingency of evolution—a debate that, unfortunately, is left untouched in this chapter.

Contingency *does* figure prominently in the third part of the book: 'Chance and Contingency in the History of Life.' In the chapter 'Contingent Evolution: Not by Chance Alone' Eric Desjardins points out that the concept of evolutionary contingency, as employed by Jacques Monod and Stephen Jay Gould, interweaves several different ideas. One of these is the idea of historicity. Desjardins gives a specific rendering of historicity, framed in terms of path dependence. He argues that three conditions have to be met for a trajectory to be path-dependent: (1) there must be alternative paths from a given initial state; (2) there must be a genuine possibility to reach alternative outcomes; and (3) at least one of the historical paths taken must be a difference maker. Desjardins nicely brings out that history can play a limiting as well as an enabling role: historical opportunities both shape and constrain the course of evolution.

Zachary D. Blount's chapter, 'History's Windings in a Flask: Microbial Experiments into Evolutionary Contingency,' considers whether Gould's thought experiment 'replaying the tape of life' has withstood experimental scrutiny. As a test case, Blount focuses specifically on Richard Lenski's long term experiments with *E. coli*. One might question whether these provide an apt test for Gould's thought experiment, which Gould typically framed in macroevolutionary terms. Blount is aware of this limitation; he provides a nuanced account of the insights that laboratorty experiments can give about the contingency of evolution.

Betul Kacar's chapter, 'Rolling the Dice Twice: Evolving Reconstructed Ancient Proteins in Extant Organisms,' takes up the same theme: putting Gould's thought experiment to experimental test. Kacar does so by going into the details of a study he has conducted, engineering an ancient protein in a modern bacterial

context. Unfortunately, irrespective of the merits of the study itself, the chapter adds little to the general findings of experimental evolution outlined in other chapters.

The final chapter by Douglas Erwin, '*Wonderful Life* Revisited: Chance and Contingency in the Ediacaran–Cambrian Radiation,' is one of the book's finest. Erwin scrutinizes the claims Gould made in *Wonderful Life*, his most provocative exposition of the contingency thesis, and argues that not all Gould's claims about the Cambrian Explosion and the Burgess Shale fossils have withstood the test of time, although some of them have. Let me comment upon two minor points of Erwin's discussion. First, Erwin rightly points out that 'the tension between chance and determinacy is plagued by issues of granularity' (293). For example, traits that may appear to be similar at a coarse-grained level of description may seem to be very different at a more fine-grained level. This is crucial to keep in mind in discussions of chance and contingency. Second, the chapter contains an historical error. On page 280, Erwin suggests that Gould took the metaphor of 'playing the tape of life again' from Conway Morris (1985), but Gould actually used the metaphor much earlier, and first stated it in print in Gould (1976) (see Sepkoski 2016).

The diversity of issues addressed in these chapters illustrates the richness of the topic at hand. The book approaches evolutionary chance and contingency from many angles and provides an excellent discussion of the following three topics: (1) the use of chance in the writings of Darwin and the synthesis scholars; (2) the sense in which evolutionary mutations are random; and (3) Gould's contingency thesis, as well as its subsequent conceptual and empirical refinements. Yet, the book's diversity, both in terms of its contents as well as the quality of its chapters, also makes it somewhat unbalanced. *Chance in Evolution* leaves ample opportunities for further, more systematic exploration.

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