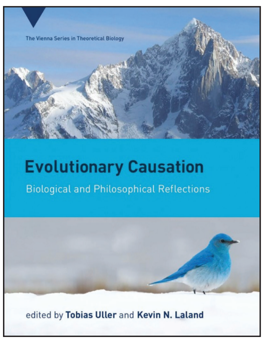
O Causation, Where Art Thou?

Evolutionary Causation: Biological and Philosophical Perspectives. Tobias Uller and Kevin Laland (editors). The Vienna Series in Theoretical Biology, 2019. 352 pp., illus. (ISBN: 9780262039925, hardcover: alc paper).

Tobias Uller (Lund University, Sweden) and Kevin Laland (University of St. Andrews, United Kingdom) have edited this interesting volume consisting of 15 chapters, in which contributors with backgrounds in evolutionary biology or philosophy discuss evolutionary causation from various perspectives. This volume emerged from a large and collaborative international research program, funded by the Templeton Foundation, with the title "Putting the extended evolutionary synthesis to test." The contributors participated in a workshop within this research program in Vienna on the theme "Cause and process in evolution."

The background is an intense discussion in the evolutionary biology community regarding the status of the Modern Synthesis, its relationship to present-day research, and whether there is a need for an update, or what has been labeled the *Extended Evolutionary Synthesis*. Some philosophers and biologists (including the editors of this volume) have argued that there is a need for an extension of evolutionary theory, claiming that traditional population and quantitative genetics do not incorporate phenomena like niche construction, developmental plasticity, developmental bias, and nongenetic inheritance (Laland et al. 2014, 2015). Other evolutionary biologists have questioned this characterization of evolutionary biology and, instead, claim that these phenomena can and have easily been incorporated into the traditional theoretical framework as various add-ons (Charlesworth et al. 2017, Futuyma 2017). For simplicity and convenience, we can label the former camp as reformers and the latter camp as traditionalists, keeping in mind that there are several intermediate conceptual positions in between these two endpoints. Indeed, one of the most interesting insights I gained from reading this volume (which is biased toward the reformist camp) is that those arguing for conceptual change in evolutionary biology are conceptually split among themselves. It is therefore difficult or even impossible to extract a single coherent message from all the contributions in this volume, although I do not think this was necessarily an aim of the editors. Perhaps it is for this reason that there is no concluding remarks chapter. Clearly, there are different voices to be heard in this debate. This volume is a good entry point in to the literature for those seeking to understand what the debate is about and what the main arguments are from the reformers' side.



The main question discussed in this volume is what should count as an evolutionary cause. Uller and Laland start out in their introductory chapter by returning to Ernst Mayr's classical distinction between *proximate* and *ultimate* explanations in biology, using his famous example of why birds migrate in autumn as an illustrative entry point. Mayr pointed out that there are several non–mutually exclusive explanations for why birds migrate. One obvious explanation is that changing day lengths and the associated changing hormonal profiles stimulate birds to migrate southward. Mayr argued that these factors are proximate causes (or *how* questions) that belong to the domains of physiology and developmental biology. Such proximate questions are the main focus of functional biologists. In contrast, *why* the birds migrate southward in autumn is an ultimate question that belongs to the field of evolutionary biology. More specifically, Mayr argued that the ultimate question of why birds migrate is based on an evolutionary process (natural selection) that has acted on genetic variation in the past and resulted in the adaptive evolution of bird migration strategies. Such bird migration strategies are nowadays manifested in genetic programs that maximize survival and reproduction.

Mayr's powerful arguments firmly established evolutionary biology as an independent biological discipline and were hugely influential. There is no question that proximate and ultimate explanations are different kinds of questions, which Uller and Laland do not deny. However, the question is whether something important was lost in setting up this distinction. Uller and Laland argue, in line with their previous work, that the proximate–ultimate distinction might have become too much of a dichotomy rather than a conceptual distinction, leading to neglect of the role of developmental processes in evolution. Developmental processes became reduced to solely proximate causes, without any status as evolutionary causes, like the classical processes of natural selection, genetic drift, recombination, and mutation (Lynch 2007). I share the concerns of Uller and Laland that it was unfortunate that developmental biology and physiology became merely background conditions in much evolutionary biology research. I see no obvious way out of this dilemma, given that proximate and ultimate causes are indeed different questions, and it therefore seems very difficult to abandon this traditional perspective introduced by Mayr. Could there nevertheless be some way out of this conceptual dilemma?

Massimo Pigliucci (chapter 2) argues that there might indeed be a way out. His proposed solution is that one could either foreground or background developmental processes, depending on how important they are in specific situations, which is entirely an empirical issue that can be solved only on a case-by-case basis. Specifically, Pigliucci argues, in the spirit of the late paleontologist Stephen Jay Gould (Gould 1980, 2002), that when developmental processes are not isotropic, they need to be foregrounded, because they are then necessary or, as he expresses it, "explanatory salient." In contrast, when developmental processes are isotropic, he argues that they can safely be backgrounded, and explanations based on natural selection are sufficient.

Pigliucci and Gould attribute the assumption of isotropic variation to the traditional viewpoint embraced by the Modern Synthesis. However, many evolutionary biologists (including myself) would strongly question this historical narrative and description of the Modern Synthesis and modern evolutionary biology (Charlesworth et al. 2017, Svensson and Berger 2019). Historically, there is little evidence for the claim that evolutionary biologists before or after the Modern Synthesis assumed that variation was entirely isotropic and that mutations were equally likely in all phenotypic directions (Svensson and Berger 2019). Instead, an alternative interpretation and historical narrative is that Gould's characterization of the modern synthesis reflected his own strong but very biased agenda that he pushed for decades (Gould 1980, 2002, Sepkoski 2012). This agenda pushed by Gould was largely based on arguments that evolutionary biology was in crisis and in urgent need of reform. Gould claimed that adaptationism (or neo-Darwinism, as he frequently called it) had been pushed too far and that the Modern Synthesis had hardened from its original and more pluralistic foundation (Gould 1980, 2002). It is only relatively recently, several decades after Gould's death, that his scientific legacy and strong agenda are starting to become more critically evaluated and discussed (Sepkoski 2012). According to Sepkoski, Gould consciously used as a career strategy to describe the Modern Synthesis in more simplistic and naive adaptationist terms than it ever was. Gould repeatedly used this caricature of the Modern Synthesis to argue for his own more pluralistic position (Sepkoski 2012). Given that many reformers (including several of the contributors in this volume) who argue for an extended evolutionary synthesis implicitly or explicitly refer to Gould's characterizations of the Modern Synthesis, I think that future debates would benefit from a more critical evaluation of Gould's long-lasting legacy and some of his questionable claims. This is not to deny Gould's importance as a popular science writer and pioneer of quantitative methods in paleobiology; these were clearly important and impressive achievements (Sepkoski 2012). But like few other evolutionary biologists (possibly with the exception of Richard Dawkins), Gould was able to set the agenda and drive debates in evolutionary biology by perpetuating a highly biased and questionable historical narrative that does not necessarily hold up to critical scrutiny.

Several authors in the present volume discuss *the standard theory* or *the standard view* of evolutionary biology, which they contrast against alternative theoretical frameworks (e.g., Arlin Stoltzfus in chapter 3, Day and colleagues in chapter 5, Sonia Sultan in chapter 6, and Richard Watson and Christoph Thies in chapter 10). Some even seem to use *the standard view*, *the modern synthesis*, and the term *neo-Darwinism* interchangeably (e.g., Arnaud Pocheville in chapter 13), which is unfortunate, because these are really different phenomena, although Yun Otsuka (chapter 12) makes some clarifying distinctions between them.

But what *is* the standard view, really? This was not entirely clear to me after reading through these chapters. The opinions seem to be divided among the contributors. For instance, Stoltzfus argues that the standard view inherited from the Modern Synthesis ignores the potential directionality of novel mutations and incorrectly assumes that standing genetic variation in a closed gene pool is sufficient to explain evolution. In contrast, Day and colleagues argue in an opposite way and emphasize that standing genetic variation deserves more attention and was maybe even neglected in the Modern Synthesis. So who is correct here? I believe that Day and colleagues give a more fair characterization of the current state of the art of evolutionary biology than Stoltzfus does. If anything, standing genetic variation has for a long time been quite neglected.

Moreover, Stoltzfus tries to reintroduce Mendelian mutationism by arguing for mutation bias as a novel evolutionary process, something that is based on several questionable assumptions. As Stoltzfus admits himself, the presence of standing genetic variation in a population makes mutation bias extremely unlikely to influence adaptive evolutionary directionality. Few evolutionary biologists question the key role of mutation bias in neutral evolution when (by definition) selection is absent. However, for mutation bias to significantly influence the direction of adaptive evolution and to a profound degree, either the population size needs to be small so that mutation bias is aided by genetic drift

(Lynch 2007), or one has to make strong assumptions about reciprocal sign epistasis (i.e., a form of effective fitness neutrality) among interacting loci (Svensson and Berger 2019). For these reasons, it appears that Stoltzfus exaggerates the empirical case for mutation bias as a directional force in adaptive evolution.

Sultan, in her chapter, instead associates the standard view with a neglect of phenotypic plasticity—particularly, transgenerational phenotypic plasticity. She discusses reaction norm evolution in depth and illustrates her reasoning using empirical examples from her own interesting research on plants. I found these empirical examples fascinating. Clearly, there is a lot of interesting future research to be done in this area, beyond plants in which these phenomena have been studied in more detail and where our knowledge is greater. However, I did not see how the study of reaction norms, however interesting it is, would seriously challenge the standard thinking among evolutionary biologists. Phenotypic plasticity is today well established, accepted, and uncontroversial in the evolutionary biology community and has been so for several decades; Sultan's arguments are therefore hardly heretical.

Watson and Thies attribute the standard view of the modern synthesis to selection, variation, and inheritance at a single evolutionary level—for example, in a population of individuals. They argue that to fully understand the causes of evolutionary transitions in individuality from one level to a new level (e.g., from a population of unicellular organisms to multicellularity), one needs to take into account evolutionary factors other than selection, variation, and heredity—most notably, niche construction. In a similar vein, Helanterä and Uller (chapter 9) discuss such evolutionary transitions in the case of social insects, which they characterize as traversing through Darwinian space. They introduce us to the interesting concept of de-Darwinization of individuals within larger collectives. Specifically, evolutionary transitions, whether from unicellularity to multicellularity or from solitary insects to social insects, tips the balance between higher-level selection of collectives and lower-level selection of individuals in favor of the former. Such higher-level units can then achieve evolutionary individuality and can evolve in larger populations of similar units through the evolutionary processes of selection and drift. These new higher-level units (collectives) can then also suppress lower-level selection of individuals (particles) within these larger collectives, because selection at such lower levels threatens to disrupt large-scale cooperation—for instance, if selfish particles promote their own reproduction at the expense of the collective; hence the term *de-Darwinization*. As Watson, Thies, Helanterä, and Uller all note, this perspective is a merging of multilevel selection theory with the theory of major evolutionary transitions. They discuss the rich and growing literature in this area. To me, these two chapters were the most interesting and thought provoking. The authors might have a point in that the standard theory and its predecessor in the Modern Synthesis have not fully accommodated such hierarchical thinking and evolutionary transitions in individuality. If Watson, Thies, Helanterä, and Uller are correct in this characterization of the standard theory (which is open for discussion), then the traditional theoretical framework of selection, variation, and inheritance becomes a special case that happens *within* given evolutionary levels. In contrast, *how* individuality evolves, they argue, is something that that the standard theory leaves out.

Several contributors discuss the phenomenon of niche construction—that is, how organisms are not passive objects of selection but actually modify their own selective environments, sometimes to their own adaptive advantage (e.g., Laland and colleagues in chapter 7, Watson and Thies in chapter 10, Yun Otsuka and Lynn Chiu in chapter 14). Niche construction is a contentious topic, with much disagreement, and this debate cannot be fully covered here. Nevertheless, Laland and colleagues argue that niche construction is a neglected evolutionary process and that the classical Modern Synthesis framework needs to change rather than expand to incorporate this. This quite radical view seems to run counter to what the same authors have said elsewhere, where they have instead argued that an extension of standard evolutionary theory would be sufficient to incorporate niche construction (Laland et al. 2015). This (unconscious?) contradiction aside, there are several issues with niche construction that are problematic, including its broad scope, which includes both nonadaptive and adaptive effects on the environment by organisms, be it adaptive structures such as the beaver dam as prime example or waste products in *Drosophila*-cultures experiencing density-dependent competition. Another common counterargument against niche construction theory is that it is neither neglected nor an evolutionary process. It was unclear to me after reading Laland and colleagues' chapter whether niche construction should be regarded as a theory (formally, niche construction theory) or merely a different perspective. I note that Laland and colleagues seem to switch between these different viewpoints in their chapter.

Since the phenomenon of niche construction is so broad, it includes essentially all the mechanisms and ways in which organisms interact and modify their local environments. This necessitates finer subdivision of different kinds of niche construction, something that is discussed in detail by Chiu in her chapter. We are told that there is *experiental* niche construction, *developmental* niche construction, *physical* niche construction, *relocational* niche construction, *mediational* niche construction, and maybe several other forms. Niche construction therefore incorporates phenomena that have previously been discussed under different scientific umbrellas and in different contexts, including development, plasticity, habitat selection, and homeostasis, to mention only a few areas. To me, this is also the main problem with niche construction as a theoretical concept if not an evolutionary process; It includes so many different (but interesting) phenomena. It therefore becomes very difficult to find any generality that holds across very different biological phenomena and processes. Otsuka discusses causal modeling and shows that niche construction can be incorporated as an extended phenotypic trait using this approach. Niche construction can therefore evolve by natural selection like other phenotypic traits, but it can also feed back on selection itself, something that can be illustrated and analyzed using causal graphs. To me, Otsuka's approach is an elegant, pragmatic, and operationally and empirically fruitful way of incorporating niche construction phenomena in evolutionary research. I suspect, however, that not everyone arguing for the importance of niche construction is entirely satisfied by this straightforward analytical way of solving the Gordian knot of how niche construction should be incorporated into evolutionary theory.

In one of the more philosophical chapters, Denis Walsh (chapter 11) discusses what he calls "the paradox of population thinking"—namely, that natural selection results from individuals that die and reproduce differentially, but evolution by natural selection is a population-level process resulting in a change in the heritable composition of populations across generations. Walsh represents the so-called statisticalist school among philosophers who have questioned the classical view of natural selection as a force, as it was originally formulated and articulated by philosopher Elliott Sober in his classical book *The Nature of Selection* (Sober 1984). Whereas Sober compared evolution by natural selection to the physical forces in Newtonian mechanics, statisticalists like Walsh instead emphasize that since it is individuals who survive and reproduce; the true causality does not take place at the level of populations. According to Walsh and the statisticalist school, evolution by natural selection is a noncausal statitistcal epiphenomenon, or a so-called higher-order effect, as opposed to the fate of individuals, which is a first order cause. The statisticalist view has been criticized by Otsuka and Sober and by the causalist school in philosophy of biology. Space does not allow me to dive deep into these criticisms, but in essence, the causalists (and presumably the majority of evolutionary biologists) reject Walsh's view. The main argument against the statisticalist view is that they conflate natural selection with evolution by natural selection and variation in fitness with selection. The statisticalists have therefore failed to realize that selection is a process resulting from causal covariance between traits and fitness (selection *for* in Sober's terminology; Sober 1984). Although Walsh and other statisticalists have raised some interesting points, their view of statistical analysis is a bit out of date—in particular with the growing recognition in recent years of how causal analysis can dissect statistical patterns such as covariance structures, something that is also discussed in Otsuka's chapter.

In summary, Uller and Laland have done an excellent job in compiling this edited volume that should be of interest to all those who wish to dwell on the high-level conceptual debates in evolutionary biology over the last decades. The main value of this volume, to me, is that it forced me to think and clarify my own views, particularly when reading chapters in which I disagreed with the contributors. This volume is also valuable because it exposes conceptual disagreements within the reformist camp. One would wish to see a similar volume published where the disagreements within the more traditionalist camp in evolutionary biology were exposed in a similar fashion. Evolutionary biology today is certainly a mature scientific field with room for several different research traditions and in which different schools of thought coexist. This book, alongside more traditionalist perspectives, could be excellent material for a cross-departmental reading group of evolutionary biologists and philosophers, who certainly have much to learn from each other.

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