

Exploring Darwinian Worlds: From Darwin to the Extended Synthesis

Essay Review of T. Heams, P. Huneman, G. Lecointre and M. Silberstein (eds): *Handbook of Evolutionary Thinking in the Sciences*, Springer, Dordrecht, 2015, 910 pp, \$349.00, ISBN: 978-94-017-9014-7

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1 Introduction

“Nothing in Biology Makes Sense Except in the Light of Evolution.” As the title of Dobzhansky’s (1973) seminal article proclaimed, evolutionary theory provides both theoretical foundations and conceptual unity to all other domains of biology. It seems a truism to assert that the majority of biologists and philosophers of biology would still agree with Dobzhansky’s tenet. But, to know how, why, and to what extent they do agree, an excellent starting point is the *Handbook of Evolutionary Thinking in the Sciences*. First published in French with the title *Les mondes darwinien* (“Darwinian worlds”), to celebrate the 150th anniversary of the publication of the *Origin of Species*, the volume is an articulated overview of contemporary evolutionary thinking, with an impressive array of topics and authors, most of whom are based in France. The *Handbook* is divided into 6 parts, respectively devoted to: processes; patterns; contributions to the philosophy of science; impact of Darwinism on central biological notions, from molecules to ecosystems; Darwinism applied to fields of research other than biology; anti-Darwinism. Each part is in turn divided into chapters—some of which are enriched by appendices—for a total of 42.

Prima facie, Dobzhansky’s motto lends itself to a trivial reading: it is just a fact that life cannot be studied but within an evolutionary framework. Yet, it is far from trivial to single-mindedly ground the motto in the specific theories and practices that make use of evolutionary thinking. The *Handbook* stands as a demonstration of the heterogeneity of approaches to even the most basic evolutionary principles,

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beginning with “descent with modification” and “natural selection.” To put some order amidst such heterogeneity, we shall single out four different ways of modifying Darwinian principles: expansion, extension, inclusion, and exportation. We borrow the first two from Jean Gayon’s *Foreword* (who in turn draws on Stephen Jay Gould 2002), and we shall refer to them as fundamental “movements” that Darwinian principles underwent since Darwin formulated them.

The first movement is *expansion*. A principle is expanded when it is revised in order to account for an increasingly broad and varied spectrum of empirical evidence over a given kind of biological process. The second movement is *extension*. A principle is extended when it is applied to newly introduced biological domains of discourse and newly devised biological entities. (Gayon includes in extension also the application of Darwinian principles to domains that are not strictly biological; we shall call this ‘exportation,’ as we explain below).

The study of Darwinian principles through the lenses of expansion and extension brings to surface at least two fundamental theoretical issues, which traverse the volume and which suggest two additional ‘movements’ of Darwinian principles over the decades. First, from the fact that all organisms and biological processes have been produced by the evolutionary history of our planet, is it legitimate to infer “that all these processes are explainable by the same set of principles” (p. 229)? Secondly, can this very same set of principles be fruitfully and legitimately exported outside biology *sensu strictu*?

The reader will not find a univocal answer to these questions in the *Handbook*; as Gayon writes (still in the *Foreword*), the book “is difficult, since it launches without concession into difficult theoretical problems, where often no consensus exists” (p. vi). Nonetheless, the *Handbook* demonstrates numerous approaches to such questions and suggests two movements in addition to those noted by Gayon: inclusion and exportation.

Inclusion has to do with the putative universal agreement on Dobzhansky’s motto. Following Delord (chap. 25), who quotes Leigh Van Valen, the father of the Red Queen hypothesis, it could well be argued that “evolution is the control of development by ecology.” Or, to put it in Delord’s words, it could well be that “evolutionary processes only comprise the result of ecological interactions on organisms subject to the laws of ontogenesis” (p. 533). Thus, it is an open question whether evolutionary theory warrants a perspective that includes all processes and entities that are key in biology or, rather, whether evolution is an aspect of some more fundamental kind of processes (e.g. ecological interactions). While it is a fact that life needs to be understood in light of evolution, it is also a fact that not the whole of biology agrees with the logical precedence of evolutionary theory in explaining and describing variation, adaptation, and complexity among living entities. The missing link between the Modern Synthesis and other disciplines (most notably ecology and developmental biology) as well as the increasing recognition of the evolutionary role played by certain phenomena (such as phenotypic plasticity, epigenetic inheritance or niche construction) left room for the request—recently advanced (see for instance Pigliucci and Müller 2010)—for a New Synthesis, which some proposed to call “Extended Evolutionary Synthesis.”

Exportation—the fourth movement—concerns domains of discourse that are not strictly (or, at least, *prima facie*) biological, such as religion and economics. Thus, while extension—as we characterized it above—concerns newly introduced biological domains of discourse and newly devised biological entities, exportation brings instead Darwinian principles outside the arena of life sciences. Only exportation has as a consequence the trans-disciplinary potential of Darwinism, namely its capability of furnishing “a common system of axioms for a set of disciplines” (Klein 2004). Accordingly, extension and exportation prompt different difficulties. In extension, the main issue is how to carry out the application of Darwinian principles. Such an issue typically leaves untouched the range of application of the principles and their scientific status, which are instead called into question in the case of exportation.

In these few pages, we are not aiming to answer the questions just raised through the four movements; rather, we suggest them as questions to keep in mind while reading the book. Accordingly, we shall divide up our review following the four movements. We, then, conclude with some remarks on the place of the volume in the contemporary literature in philosophy of biology.

2 Expansion: The Principles of Darwinism and Their Revision

If what draws us to the *Handbook* in the first place are the principles of Darwinism, then a good starting point for our exploration is Chapter 11, by Anouk Barberousse and Sarah Samadi. In this chapter, the authors propose a formalization of evolutionary theory as currently used today in empirical research, arguing—contra Smart (1936)—that evolutionary theory can be as good a scientific theory as widely accepted physical theories. Barberousse and Samadi mold their view around one of the first post-synthetic formalizations of evolutionary theory by natural selection, which is due to Richard Lewontin and dates back to 1970. According to Lewontin, the theory has three chief principles: (1) phenotypic variation; (2) differential fitness; (3) heritability of fitness; also suggesting that “it is important to note a certain generality in the principles: no particular mechanism of inheritance is specified, but only a correlation in fitness between parent and offspring” (pp. 241–242). This generality is what allows Darwinian principles to ‘move’ the four ways described above. Hence, it is also the reason why not only natural selection itself (magisterially illustrated by Philippe Huneman in Chapter 4), but all of these principles—so simple and intuitive—have proven an inexhaustible source of theoretical difficulties and empirical controversies (for a witty example from the *Handbook*, see Chapter 24 on the evolutionary costs of small stature for *Homo sapiens* women, by Priscille Touraille). Thomas Heams takes on the difficult task—that the author managed effectively, giving us two clear and useful chapters—of presenting two of the fundamental Darwinian principles: variation (Chapter 2, that we suggest to read together with Chapter 5 by Philippe Grandcolas, Chapter 7 by Véronique Barriol, and Chapter 12 by Pascal Charbonnat) and heredity (Chapter 3, to be read with Chapter 9, by Guillaume Lecointre).

3 Extension and Inclusion: Towards a New Synthesis?

The history of biology offers at least two turning moments in the theoretical extension of Darwinian theory to novel domains of discourse within the life sciences. The first occurred when the theory of descent was applied to molecular structures, producing a shift in focus from organisms to their molecular parts. Such a shift in focus shook the theory to the core. Among other things, the shift called for a rethinking of both the scale of the fundamental patterns and processes of evolution and the main entities that they involve. The second turning moment was brought forth by the affirmation of ‘population thinking,’ which changed the methods through which subjects such as economics would be studied from an evolutionary perspective (on evolutionary economics cf. Chapter 38 by Eva Debray).

Despite such turning moments, which extended Darwinian theory in important ways, it is still an open question whether evolutionary biology can come to include in the scope of its principles the entire spectrum of biological processes and entities. Do Darwinian principles really act as the cornerstones of biology, on the basis of which to account for the existence and variety of any biological process or entity? This is the challenge of inclusion, which most vividly emerges in PART III and IV of the *Handbook*. Since their original formulation and their alleged completion in the 1930s with the Modern Synthesis, the principles of evolutionary theory have undergone important revisions, a process that has brought to the integration of new concepts in the theory, such as—to give but one example—genetic drift (cf. Chapter 17, by Christophe Malaterre and Francesca Merlin, which explores the stochastic character of evolutionary theory and its origin). The extent of the revisions needed to accommodate new findings in the Modern Synthesis gene-based framework has brought some scholars to call for a change in how evolution is conceptualized. This would not imply a shift of paradigm in the Kuhnian sense (Pigliucci 2007), but rather an “alternative vision of evolution...in which the processes by which organisms grow and develop are recognized as causes of evolution” (Laland et al. 2014). According to other scholars, on the contrary, evolutionary theory, as it is, is perfectly capable of accommodating those data.

The one just described is the core of one of the most stimulating debates in contemporary philosophy of biology. The positions of the two opposed parties were most notably presented in a double article appeared in 2014 in *Nature*—*Does Evolutionary Theory Need a Rethink?* (cf. Laland et al. 2014). To understand the background and the nature of the debate, the *Handbook* proves to be a crucial resource, in particular in virtue of the chapters devoted to examine those concepts and disciplines whose inclusion in the traditional framework of evolutionary theory would imply “an alternative vision of evolution.” Among such disciplines we need to discuss at least three cases: ecology, systems biology, and developmental biology.

Even though ecology was implied in the Modern Synthesis, ecologists and evolutionary biologists followed independent paths, and still today ecological theory rarely features in evolutionary study, in part because of the putative mismatch between ecological and evolutionary time scales—analyzed in detail in the already mentioned chapter by Delord. Niche construction theorists, in particular, who are

among the partisans of the Extended Synthesis, argue for the inclusion of the concept of niche construction (see chapter 26 by Arnaud Pocheville, which traces the history of the concept of the ecological niche focusing on its explanatory power of biodiversity and species coexistence patterns) in the Extended Synthesis framework as an evolutionary mechanism that goes hand in hand with natural selection and that cannot be reduced to it.

Another discipline the Extended Synthesis aims at including is systems biology, which many evolutionary biologists regarded as too general and incapable of producing sufficiently specific empirical hypotheses. Still, as Pierre-Alain Braillard argues—mainly on the basis of the problem of artifact thinking in biology—in the Conclusions of Chapter 16, “...systems biology could benefit from a genuine evolutionary reflection. Inversely, it should also be clear that evolutionary biology will most probably be able to find an important help for future progress in systems biology’s new methods and concepts.”

But the most striking absence in the Modern Synthesis framework was developmental biology (Pigliucci 2007). Despite pioneering attempts to coalesce development and evolution, such as (Goldschmidt 1940), the developmental perspective remained by and large out of the picture at least since Gould’s (1977) book, *Ontogeny and Phylogeny*. Between the 1980s and the 1990s, the research program of Evo-Devo arose with the aim of studying both the evolution of development and the developmental basis of evolution, supplying the Modern Synthesis, mainly a theory of genes, with what Popper has called for, namely a theory of forms (Pigliucci 2007). Evo-Devo is a field dense of philosophical implications, surrounding most notably concepts such as phenotypic plasticity (of which Antonine Nicoglou offers a stimulating philosophical treatment in Chapter 14), evolvability, novelty, and modularity, as Alan C. Love shows in Chapter 13. Indeed, Evo-Devo is probably the research program that “brings major new elements for a ‘new synthesis’ of the theory of evolution”, as Guillaume Balavoine states in Chapter 21. Balavoine’s rich and complex chapter brings together recent findings within different branches of biology (e.g. the discovery of conserved developmental genes in phylogenetically distant groups) and the study of the molecular mechanisms of the evolution of development. In the chapter, Balavoine’s convincingly shows that such findings are an important step in proceeding not only towards an integration between evolutionary and functional biology (as clearly illustrated in Chapter 15, by Michel Morange), but also an integration towards “the reconstitution of animal body plan history in a comprehensive phylogenetic tree.” It is worth noticing that molecular biology’s findings impact theories of both evolutionary development and phylogenesis. Since Darwin proposed a phylogenetic tree—the only illustration in the *Origin*—that associates patterns and processes (i.e. the kinship structure and speciation processes), various treatments of such association have been proposed. These treatments are meticulously reconstructed in Chapter 18, by Pascal Tassy (that we suggest to read together with Chapter 8, on species, by Sarah Samadi and Anouk Barberousse), who puts an emphasis on more recent developments of phylogenetics (in particular on Hennigian phylogenetics and subsequent cladistics and probability approaches).

Can evolutionary principles be adequately extended to cover all domains of discourse within biology? Or, rather, shouldn't we more modestly admit that such principles cannot account for *any* biological process or entity, as not every subfield of biology is included into evolutionary theory? By tracing the multifaceted guises of contemporary evolutionary thinking, the *Handbook* thereby displays also some of the limitations of such thinking. Indeed, the principles of evolution have been applied to many fields in the life sciences, but to date they still fail to be adequately squared with topics such as development, molecular structures, or diseases and medicines (cf. for instance Chapter 20, by Thomas Heams, the already mentioned Chapter 21, and Chapter 27 by Pierre-Olivier Méthot).

4 Exporting Darwinism

The *Handbook* contains a wealth of resources for approaching the ever changing and plastic core of Darwinism, in its applications to biological entities and processes. Equally impressive are the number of approaches and suggestions which are found in the volume and which help us grapple with the *exportations* of Darwinism. Since the earliest formulations of the theory, Darwinian principles were applied to domains of investigation that did not directly or solely involve living entities, such as languages and artifacts (e.g. music and figurative art). Over time, however, as the key principles of the theory kept being 'exported' (in the sense explained above), so the approaches to Darwinian exportation kept being revised. It is thus useful to study the differences between exportations of Darwinian principles across the decades and centuries. For instance, comparing the way in which Darwin or one of his contemporaries applied evolutionary theory to the history of language or economics, and the way in which contemporary evolutionary thinking approaches those subjects, reflects the changes in how the principles of the theory have been understood. In this sense, the study of exportations of Darwinism may shed light on how Darwinism can and should be exported.

The *Handbook* contains plenty of examples of exportations of Darwinian principles: computer science (Chapter 28, by Marc Schoenauer), robotics (Chapter 29, by Nicolas Bresseche), economics (the already mentioned chapter 38), social science (Chapter 37, by Christophe Heintz and Nicolas Claidière), and linguistics (Chapter 39, by Mahé Ben Hamed). Moreover, a block of five chapters (from 30 to 34)—introduced by Chapter 30, by Philippe Huneman and Edouard Machery—is devoted to different aspects, and possible theoretical difficulties, of the exportation of Darwinian principles to evolutionary psychology. Chapter 31, by Stephen M. Downes, tackles the issue of the viability of the evolutionary psychologists' notion of adaptationism as an organizing principle for their research; Chapter 32, by Pierre Poirier and Luc Faucher explores the externalist conception of evolutionary psychology arguing for an integration between cognitive science and evolutionary biology; Chapter 33, by Jean-Louis Dessalles analyses the peculiarity of human language compared to the forms of sharing information of other animals; and Chapter 34, by Christine Clavier, offers an exploration of the often misunderstood field of evolutionary ethics. This last chapter can be usefully read in connection with

three chapters (within the same section of the *Handbook*), which reach beyond the confines of philosophy of science. Chapter 35, by Jérôme Ravat, goes through Darwin's *Descent of Man*, trying to "dispel some relapsing misconception" about Darwin's view on the emergence of morality in our species. Chapter 36, by Pierrick Bourrat, explores the evolution of religion, offering a critical discussion of the theories that explain religious phenomenon on the basis of cooperation. François Longy, in a philosophically inspiring chapter, presents teleosemantics, that is the research program established in the 80s with the intent to explain thought and language in naturalistic terms, by putting in relation mental content and linguistic meaning with biological functions (e.g. Does the dance of a bee has a *signification*? Is our capability of *meaning* something a derivate of some natural property?).

It would be an interesting exercise to compare those exportations with respect to how each of them draws on different (or similar) exportations of the key principles of the theory; little help is offered by the volume itself on how to solve, or approach, such exercise. In this sense, the *Handbook* is much more akin to mirror the Darwinian worlds, rather than being a travel guide to them. It is an instrument of extraordinary value for those who already know what to look for in the intellectual battlefield of evolutionary explanations.

5 Conclusion

The *Handbook* is the most comprehensive volume to date in English on the metaphysics and epistemology of the life sciences. It is a volume bringing forth the perspective of mostly Francophone researchers, many of which are "juniors." It has a thin structure, which allows for multiple reading paths of (some of) the 42 chapters. Some of these reading paths have been suggested in this review, but the reader will have fun in constructing a personal trajectory through the terrific amount of theoretical insights.

A yet unmentioned use of the *Handbook* is showcased by the last two chapters, respectively devoted to the battle against creationism (Chapter 41, by Olivier Brosseau and Marc Silberstein), and the teaching of evolutionary theory in secondary schools (Chapter 42, by Corinne Fortin). The *Handbook* stands indeed also as a precious resource for teachers of Darwinian thinking, who can quite easily single out different chapters to update their view on evolution. Under this regard, it is important to remind of a cluster of chapters on foundational topics, which seem particularly suitable for teaching purposes: Chapters 6 on function, by Armand Ricqlès and Jean Gayon; Chapter 10 on life, by Stéphane Tirard; Chapter 19 on the ways in which stories of life (beginning with the tree of life) are told, by Guillaume Lecointre; Chapter 22 on behavior and evolution, by Henri Cap; Chapter 23 on sex and evolution, by Pierre-Henri Gouyon, Damien de Vienne, and Tatiana Giraud.

If the strength of evolutionary theory rests in its plasticity to encroach on different domains and sizes of entities and processes, and if its success rests on its repeated and multifarious application to different case studies, then the hope is that more groups of researchers will follow the lead of the editors and authors of this *Handbook*.

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