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BOOK REVIEW

The Softening of the Modern Synthesis

Julian Huxley: Evolution: The Modern Synthesis; The Definitive Edition. Massimo Pigliucci and Gerd B. Müller (eds): Evolution—The Extended Synthesis

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The Modern Synthesis has been receiving bad press for some time now. Back in 1983, in an article entitled "The Hardening of the Modern Synthesis" Stephen Jay Gould criticized the way the Modern Synthesis had developed since its inception in the 1930s and early 1940s (Gould 1983). Back then, those who would later become known as 'architects' of the synthesis were united in their call for explaining evolution at all levels in terms of causation at one level: genetics. What drove changes in gene frequency remained an open question. It could be mainly selection, or drift, or some (other) form of constraint. But in the two decades that followed, the synthesis underwent a major change. By the late 1940s the synthesis had 'hardened' around adaptationism, according to Gould. Influential contributors like Dobzhansky, Simpson and Wright had increasingly expressed adaptationist views in the later editions of their landmark books. Not because evidence had piled up, showing that selection was in fact pervasive. Instead, Gould argued, adaptationist tendencies had been preserved by some kind of cultural inertia, and were now being revived. "Certain 'national styles' persisted from the eighteenth century, through Darwin's era, and into our own time. Views on adaptation provide a good example" (Gould 1983).

Gould did not just argue that some form of adaptationism had resurfaced. He became well-known for his efforts to intervene on this status quo by attempting to make evolutionary biology more 'pluralistic'. In collaborative work with Richard Lewontin (Gould and Lewontin 1979), Elisabeth Vrba (Gould and Vrba 1982; Vrba and Gould 1986) and Niles Eldredge (Eldredge and Gould 1972; Gould and Eldredge 1977) he criticized the synthesis for its adaptationism and its lack of

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appreciation for hierarchical perspectives. Gould exerted his influence in a different way as well. Together with Eldredge, he had facsimiles reprinted of the first editions of two books that had shaped synthesis, but with their own critical introductions (Eldredge 1982; Gould 1982). Dobzhansky's *Genetics and the Origin of Species* and Mayr's *Systematics and the Origin of Species* appeared as reprints in the 'Columbia Classics in Evolution' series, sending an unambiguous message to the readers: these are foundational works, but they have been superseded.

In the summer of 2008, some 25 years after Gould made his point about the hardening of the Modern Synthesis, a group of sixteen biologists and philosophers gathered at the Konrad Lorenz Institute for Evolution and Cognition Research (KLI) near Vienna, Austria, to discuss cutting-edge research that reaches beyond the synthesis framework. Before it even started, this workshop on the 'Extended Synthesis' had already attracted a fair share of attention in the blogosphere and had resulted in a news feature in *Science* (Pennisi 2008). After the meeting, *Nature* weighed in on the matter (Whitfield 2008). The results of over 3 days of presentations and extensive discussion have now been published as *Evolution—The Extended Synthesis*.[1] The publication of this collection of sixteen essays is accompanied by the republication of Julian Huxley's *Evolution: The Modern Synthesis*; the book that introduced the term 'Modern Synthesis'. Both books are introduced by the organizers of the KLI workshop, Massimo Pigliucci and Gerd Müller.

Like Gould and Eldredge before them, Pigliucci and Müller did not reissue one of the canons of the Modern Synthesis without giving the readers some 'guidance'. Starting with the cover, the editors proclaim boldly that this is 'the definitive edition' of Huxley's book. In a new foreword, they sketch the context in which the book was written and assess some of its features. They voice some mild criticism of alleged 'adaptationism'. But their tone is different from that of Gould and Eldredge. Pigliucci and Müller praise Huxley for his pluralistic outlook, which has again become essential in the forging of an Extended Synthesis. That makes Huxley's book more than just an interesting but obsolete classic. Instead, it can teach valuable lessons about how to 'soften up' a synthesis that has become hardened over time.

1 Evolution: The Modern Synthesis

Arguably, *Evolution: The Modern Synthesis* has been unparalleled by other synthesis works in its remarkable breadth and depth. In over 700 pages Huxley discusses a multiplicity of themes that would be part of the emerging Modern Synthesis. As Pigliucci and Müller perceptively observe, what is striking about this book is its pluralistic treatment of many topics compared to the better known synthesis books. For example, Huxley was much more appreciative of the controversial work of Goldschmidt than others had been and would be. He was

[1] For full disclosure, I should mention that I attended the workshop. As a Junior Fellow at the KLI at the time, I listened in on the presentations and took part in some of the discussions. I was neither involved in organizing the workshop, nor in producing its proceedings.

also expressly critical of the 'biological' species concept, which was unnecessarily restrictive to his taste. He had already criticized this species concept before, in his introduction to the collection he edited on *The New Systematics*. He complained that the exclusion of "many groups, especially among plants, universally recognized as species" by the biological species concept was to "rob the term species of its previous meaning." (Huxley 1940, 17). Not just the meaning of the term 'species' was hijacked by Dobzhansky and Mayr, the notion of the 'New Systematics' also became reframed to fit the biological species concept only (e.g. Mayr 1942, 7, 1964). In some sense, the same happened to the Modern Synthesis when it hardened in the hands of others and lost its association with Huxley's pluralistic outlook.[2]

The general tenor of *Evolution: The Modern Synthesis* is best illustrated by those passages in which he warns the reader to be careful not to draw conclusions for all of biology based on the findings from one subdiscipline. Take paleontology:

> All that paleontology can do …is to assert that, as regards the type of organisms which it studies, the evolutionary methods suggested by the geneticists and evolutionists shall not contradict its data. For instance, in face of the gradualness of transformation revealed by paleontology in sea-urchins or horses it is no good suggesting that large mutations of the sort envisaged by De Vries shall have played a major part in providing the material for evolutionary change. Even here, however, let us be careful to note the restriction imposed by the phrase "as regards the type of organism which it studies". The main lines of evolution in the more abundant forms of sea-urchins, horses, and the like may depend upon gradual change: but this is no reason for assuming that this holds for all organisms. (MS, p. 38)[3]

And more generally:

> No single formula can be universally applicable; but the different aspects of evolution must be studied afresh in every group of animals and plants. We are approaching the time when evolution must be studied not only broadly and deductively, not only intensively and analytically, but as a comparative subject. (MS, p. 46)

> Comparative Evolution is destined to become as important a branch of biology as Comparative Anatomy. In any such general survey, other aspects of evolution would demand the same comparative treatment as that accorded to genetic systems and other peculiarities of the evolving organism. (MS, p. 128)

Unlike some other contributors to the synthesis, Huxley was very cautious about making sweeping claims on the basis of fruit flies in a lab in New York, or birds in the Southwest Pacific.

The final two chapters of Huxley's book may be expected to invite more skepticism from a contemporary point of view, for there he discusses 'evolutionary trends' and 'evolutionary progress'. Under the heading of evolutionary trends, he

[2] See Beatty (1992, 186–188) for a discussion of Huxley's resistance to going along with this trend.

[3] As shorthands for references to the two books reviewed here, I will use (MS, p. [pagenumbers]) and (ES, p. [pagenumbers]).

directs attention at phenomena like adaptive evolution and *consequential evolution*. The latter concept is essentially "an attempt to account for the directional effects of ontogenetic development." He invokes work on allometry, heterochrony and Goldschmidt's notion of 'rate genes' to account for (differences in) body form. In their new introduction to Huxley's book, Pigliucci and Müller observe that despite the importance and originality of this discussion "it took nearly half a century until it was taken seriously by the research program of Evo-Devo." (MS, p. 5). Also interesting is Huxley's explanation of adaptive evolutionary trends. They are the result of *orthoselection*, the functionalist-externalist counterpart to orthogenesis. Huxley is strongly critical of orthogenesis, which posits an intrinsic drive (or inertia, as you will) to evolve in a predetermined direction. Some of the patterns orthogeneticists have described are real, but the orthogenetic processes that cause them are not. However, orthoselection *can* promote the continuation of an adaptive trend once it has been initiated. Huxley's explanation for how this happens sounds remarkably similar to what has become known in philosophical circles as generative entrenchment (Wimsatt 2001, 2007): "A specialized line …finds itself at the bottom of a groove cut for it by selection; and the further a trend towards specialization has proceeded, the deeper will be the biological groove in which it has thus entrenched itself. Thus specialization, in so far as it is a product of natural selection, automatically protects itself against the likelihood of any change save further change in the same direction." (MS, pp. 500–501). The ensuing elaboration shows that Huxley had a quite sophisticated, probabilistic understanding of this principle, which he also referred to as the 'groove effect' (MS, p. 523).

Keenly aware of the skeptical responses talk about evolutionary progress would trigger, Huxley spent several pages clearing ground for his own treatment of this topic. He argues that accusations that progress is a subjective concept, or that is objective but falsified, or that it requires positing an non-existent Law of Progress do not apply to his discussion of evolutionary progress. Moreover, he stresses that his notion of progress excludes purpose. "The task before the biologist is not to define progress a priori, but to proceed inductively to see whether he can or cannot find evidence of a process which can legitimately be called progressive …Thus evolution may perfectly well include progress without being progressive as a whole." (MS, p. 558). In Huxley's eyes, what can legitimately be called progressive is the evolution of 'higher' organisms from 'lower' ones. After all, "even the hardened opponents of the idea of biological progress find it difficult to avoid speaking of higher and lower organisms, though they may salve their consciences by putting the words between inverted commas." (MS, pp. 558–559). Hence, the distinguishing marks of higher organisms serve as a basis for his characterization of evolutionary progress. At this point, the subjectivity he said was not part of his definition has already entered through the backdoor. Unsurprisingly then, we learn in the next few pages that the pinnacle of progress has been the evolution of mankind and its culture.

Nevertheless, there are glimmerings of deeper insight in Huxley's discussion of evolutionary progress. With some imagination, we can read certain passages as hinting at a concept that has only been articulated recently. For in places, Huxley seems to characterize progress as what we would nowadays call *evolvability*. In

Huxley's view, it was not adaptation, specialization, or complexity that set the 'higher' apart from the 'lower,' but "a capacity for branching out into a multiplicity of forms," (MS, p. 559) or "characteristics … making for greater control over the environment and … making for greater independence of changes in the environment." (MS, p. 562). I am not suggesting that we should read Huxley to increase our understanding of evolvability, but rather that we should not reject outright everything he said about progress. There is *some* continuity between his notion of progress and our notion of evolvability.

Pigliucci and Müller are positive about Huxley's discussion of progress, but they do not provide much more guidance towards its contemporary importance other than saying that it is "not necessarily a satisfactory state of affairs" that the idea of progress is shunned today (MS, p. 6). The only aspect of the book they criticize explicitly is its adaptationist stance. But even in this respect sympathy for Huxley's position reigns. After all, we should not forget that Huxley was battling Lamarckism and orthogenesis, and did so by stressing the power of selection. Moreover, our more advanced understanding of genetic and developmental constraints was not available to Huxley.

Evolution: The Modern Synthesis has been updated twice to account for new developments. In 1974 it was still possible to write a long new introduction to account for new developments, but according to Pigliucci and Müller, recent advances cannot be appended in a similar way. Therefore, they present *Evolution—The Extended Synthesis*.

2 Evolution: The Extended Synthesis

This book consists of seven parts: an introduction, and six sections with two or three chapters each. The section themes range from very general to quite specific. Starting with 'Variation and Selection,' we successively encounter 'Evolving Genomes,' 'Inheritance and Replication,' 'Evolutionary Developmental Biology,' and 'Macroevolution and Evolvability.' The book appropriate concludes with a section exploring some 'Philosophical Dimensions'.

For collections like this one, there is no single ideal way of partitioning the essays into sections. Nevertheless, the present classification is rather odd in some ways. Why, for instance, is evolvability as a section theme severed from evolutionary developmental biology (evo-devo), though it is often regarded as the organizing theme of evo-devo (e.g. Hendrikse et al., 2007)? Anyway, given that choice it is remarkable that the essay that opens evo-devo section ('Facilitated Variation', by Marc Kirschner and John Gerhart) is explicitly about evolvability. On the other hand, one of the essays that appears in the section on Macroevolution and Evolvability ('Origination Patterns and Multilevel Processes in Macroevolution', by David Jablonski) seems much closer in theme to a much earlier essay, from the Variation and Selection section ('Multilevel Selection and Major Transitions', by David Sloan Wilson), since both essays focus on multilevel selection.

In defense of the editors, the alternative ways in which the sixteen essays could have been arranged is an indicator of the complex web of relations that exist

between the various topics. Exploring these relations is one the purposes of the book, as the editors make clear in the introduction. Their first stab at characterizing the current state of evolutionary theory is presented as a diagram composed of three concentric circles. The innermost circle contains the 'key concepts' of Darwinism (variation, inheritance, natural selection), circumscribed by those of the Modern Synthesis (e.g. population genetics and speciation), with the distinguishing features of Extended Synthesis in the outer ring (e.g. evo-devo, niche construction, genomics, and other themes from the book). Furthermore, they point out that the hallmark of the Extended Synthesis is the "ongoing a shift from a population-dynamic account to a causal-mechanistic theory of phenotypic evolution." (ES, p. 12). Because of this different focus, the Extended Synthesis is also liberated from three "basic restrictions and methodological commitments that had been necessary for the correlational approach of the Modern Synthesis to work." (ES, p. 12). 'Gradualism' gets mentioned as a commitment that is questioned by the study of complex dynamical systems. 'Externalism' and 'gene-centrism' were constitutive constraints of the Modern Synthesis, but not of the new synthesis in the making.

Next comes the meat of the book, with 14 chapters presenting the content of the Extended Synthesis. They range from the historically-oriented and more formal chapters to ones which review a wealth of recent empirical discoveries. One chapter combines all these perspectives. Chrisantha Fernando and Eörs Szathmáry discuss the relevance of evolutionary theory for neuroscience by presenting "a truly evolutionary approach to brain function in the higher vertebrates" (ES, p. 209). Szathmáry, well-known among theoretical biologists for bringing chemistry to the table in his magisterial work on the major transitions with Maynard Smith (Maynard Smith and Szathmáry, 1995), also approaches neuroscience from chemistry. The authors discuss simple and more complex chemical replicators as a basis for a discussion of neuronal replicators. Using the work of Changeux (1985) and Edelman (1987) as stepping stones, they launch into a discussion of Hebbian learning, neural topology and issues like the Hierarchical IF-and-only-IF problem. For the outsider it is easy to get lost in these informed, but complex issues that span chemistry, theoretical biology, computer science and neuroscience. Although it is the longest chapter of the book, forty pages are hardly sufficient for exploring this relatively barren terrain while speaking to a broad audience.

Jablonka and Lamb 2005, as well as Kirschner and Gerhart 2005 perform well at speaking to a non-expert audience. Their contributions are extracts and extensions of their celebrated semi-popular books. Those who do not have the time to stay up-to-date on the rapidly expanding knowledge on cellular epigenetic inheritance systems will benefit from the chapter by Jablonka and Lamb. A novel conceptual toolkit for understanding how phenotypic variation is generated is laid out lucidly by the systems biologists Kirschner and Gerhart. Both essays also provide a compact discussion of the historical dimensions of their subjects.

Philosopher of science John Beatty presents the most historically-oriented chapter, in which he reconsiders the meaning and importance of 'chance variation'. An informed analysis of the role of chance variation in evolutionary theory from Darwin to Gould is followed by a discussion of recent experimental work on *E. coli*, which evidences that the order of appearance of chance variations alone can

influence the direction of evolutionary change—biased variation or directed selection are not required for it. It would have been helpful if Beatty had linked his historical discussion more explicitly to themes in evo-devo. For example, an exploration of the relation to the literature on directed variation in embryos (e.g. Wallace 2004) would have tightened the integration of this chapter with the others. Such an extension could have helped to clarify why it is important to trace the development of certain themes from (pre-)Darwinian days to today. As it stands, Beatty's discussion is (too) easily criticized for being out of touch with current developments. Indeed, during the workshop in 2008, Marc Kirschner responded to Beatty's presentation by requesting to leave a reassessment of Darwin's ideas out of the discussion and to look ahead instead.

Pigliucci, in his chapter on phenotypic plasticity, repeats the famous point by Lewontin (1974) that: "from a reaction norm perspective, it simply makes no sense to attempt to separate genetic from environmental effects, because the 'genetic,' 'environmental,' and interaction variances are all properties of the specific genotype-environment combinations that are characteristic of a given population of organisms." (ES, pp. 355–356). He refers to the discussions of Jablonka and Lamb, Odling-Smee, Müller, and Newman at several points, showing that all these are closely interrelated. Newman, for example, directs our attention to the physical and chemical aspects of functional modules that come in play in the development of multicellular organisms. In a rather technical discussion, he elaborates how interactions and modifications of these so-called 'dynamic patterning modules' (DPMs) can help explain origination of new forms, especially for the early, 'pre-Mendelian' days of the Metazoa. His evolutionary perspective includes genetics, but downplays its role. The way in which DPMs generate form are also influenced by a host of other factors, ranging from the physical and chemical to the ecological, giving an important role to phenotypic plasticity as a factor in evolution.

Pigliucci, like Newman, is convincing in showing that phenotypic plasticity is a *potentially* important factor in macroevolution. But at this stage, it seems fair to be somewhat skeptical about the role phenotypic plasticity has played in the evolutionary process in general. Plasticity might, for instance, have been crucial factor in the origin of multicellularity, only to have disappeared from center stage later on. A piecemeal approach to studying phenotypic plasticity is called for. Therefore, it may do more harm than good to emphasize the importance of this research by giving in to speculation. Pigliucci does not shy away from some speculative musings, although he is upfront about the fact that they are exactly that. About a picture of a bipedal macaque with paralyzed upper limbs, he remarks: "It is hard to stare at pictures like this one and not think that perhaps this sort of phenotypic plasticity is what first opened the way to the evolution of bipedalism in hominids. This is, of course, speculation, but surely a very tempting one." (ES, p. 369). Surely, many others would find it almost impossible to imagine that this *is* how the transition to bipedalism was made. Musings like these are grist for the mill of skeptics about evolvability in general and distract from the importance of approaching evolvability research in a piecemeal fashion.

Pigliucci and Newman are among those who believe that the population genetic framework on which the Modern Synthesis rests faces substantial challenges in light

of recent research. It cannot capture, or do justice to the complexity of multi-channeled inheritance, multi-level selection, and the complex interactions between developmental components. But not all contributors feel this way. In their chapter on Evolution of Evolvability, Wagner and Draghi stress the resilience of population genetics, illustrated by its capacity to embrace new concepts: "[T]he idea of evolution of evolvability is not as radical a break from the tradition of populations genetics theory as some population geneticists may think. The neglect of evolution of evolvability by the research program of the synthesis is more a self-inflicted blind spot rather than dictated by a real limitation of the conceptual framework of population genetic theory itself." (ES, p. 379–380). The population genetic models they discuss show that, under certain circumstances, evolvability is evolvable. Hence, they conclude that "there are no deep conceptual obstacles for population genetic theory to explain the evolution of evolvability." (ES, p. 396). Thus, although the study of 'evolvability' is a recent development, it can be carried out within a population genetic framework.

More outspokenly critical of the notion of an Extended Synthesis is Sergey Gavrilets. His chapter, 'High-Dimensional Fitness Landscapes and Speciation,' evaluates how models of highly-dimensional fitness landscapes challenge—or at least, allow us to refine—some of the conclusions drawn from the less advanced three-dimensional fitness landscapes that have pervaded the Modern Synthesis literature. Gavrilets's work falls squarely within the domain of population genetics. It is a continuation of a successful approach, rather than a break with the Modern Synthesis. Therefore, Gavrilets is skeptical about the prospects for an Extended Synthesis.

> Do new developments and knowledge really challenge the ideas central at the time of the Modern Synthesis and require a dramatic reevaluation of the basics? Definitely not. Declaring the Modern Synthesis or the Darwinian theory dead, wrong, or in crisis because some of the beliefs or views held previously are not supported by newer data or theories, or because there are still gaps in our knowledge, means being ignorant of how the science develops. Do new developments and new knowledge in different ares of biology justify the need for something that can be called an Extended Evolutionary Synthesis? I think the answer to this question is a very subjective matter. (ES, p. 72)

In defense of the other contributors, none of them proclaim the Modern Synthesis "dead, wrong, or in crisis". But Gavrilets's somewhat dissenting voice is a welcome contribution if we wish to assess what, if anything, we should understand by the Extended Synthesis. Other skeptical contributions would have been welcome, though it is understandable that the organizers of the workshop chose not to go down that road. Their goal was to explore the concept and contours of an Extended Synthesis, not to enter the arena with too many skeptics who would block an early exploration.

Before concluding with a look at the chapters on Philosophical Dimensions, let me make a few general remarks about the book. I mentioned earlier that the perspectives of the chapters differ, ranging from the more historical to the empirical

and the formal. This diversity is welcome. More troublesome is the diversity in the audiences the different participants seem to be addressing. Some, like Wagner and Gavrilets, do an excellent job at presenting complex formal models in an accessible format for a wide audience. Wray and Purugganan also deserve credit for packing a lot of recent insights from genomics into a small number of pages without losing themselves in the details. These authors speak to readers informed in evolutionary biology, but do not assume any detailed knowledge about the sub-domains they are discussing. Others aim rather low. Sloan Wilson's chapter on Multilevel Selection and Major Transitions does rather little to explain *how* multi-level selection theory has regained terrain, after having been suppressed by the Modern Synthesis. A more theoretical and less historical-descriptive chapter could have helped to put remarks made in other chapters in perspective, like Wagner's claim that there still is "a widespread belief that group selection is a weak evolutionary force" (ES, p. 386). Yet others aim too high. I already mentioned Fernando and Szathmáry in this regard. Newman's chapter also quickly becomes too technical for non-experts.

In defense of these authors, it should be said that it is somewhat unclear what the intended readership of this volume is. In the editors' introduction we read that the essays are "a beginning of a response" to oft-heard questions from their departmental colleagues about why an Extended Synthesis is needed (ES, p. 4). On the other hand, their are many signals indicating that they are targeting a much wider audience. Take the republication of the Huxley's *Evolution: The Modern Synthesis* as a companion volume and the decision to publish both works in paperback only.

3 Philosophical Dimensions

Almost all the contributors to *Evolution—The Extended Synthesis* conclude their essays with some remarks about the idea of an Extended Synthesis. Some go further, by spending a considerable amount of ink on laying out in which respects the Modern Synthesis is being challenged. Jablonka and Lamb, for example, reach beyond the topic of their own essay by presenting a list of seven assumptions that were built into the Modern Synthesis, but which are now being challenged. Their list has much in common with the points the editors raised in the introduction, but reaches further. For example, they include research that challenges the 'tree of life' pattern in their outlook on the Extended Synthesis. Other contributors bring a rather different conception of the Extended Synthesis to the table. Fernando and Szathmáry make a useful distinction between two ways in which the synthesis can be extended: laterally and vertically. "Lateral extensions transfer the thought patterns and the methodology of evolutionary theory to different, previously nonevolutionary disciplines …Vertical extensions deepen our knowledge in traditional areas of evolution research such as EvoDevo, niche construction, epigenetic inheritance, and multiple levels of selection," (ES, p. 209). Most of the chapters discuss vertical extensions. Their own chapter explores a lateral extension. Fernando and Szathmáry's distinction does not entail that lateral and vertical extensions are mutually exclusive. We could, for example, first extend evolutionary

theory vertically and then export it, laterally, to other disciplines. That is in fact what a number of the other contributors attempt to do. Sloan Wilson thinks that this is where major transitions research should be heading towards. He sees human evolution, leading to human culture, as the most recent evolutionary transition. Jablonka and Lamb and Odling-Smee, in this volume and elsewhere (Jablonka and Lamb 2005; Odling-Smee et al. 2003), also extend their vertical contributions laterally, by showing the implications of extended inheritance and niche construction for the domain of cultural evolution. What sets Fernando and Szathmáry's own lateral extension apart is that it is largely based on a barebones replication and selection framework. Rather than first extending the synthesis framework vertically, like the others do, they strip it down to its basics logical skeleton before applying it to neuroscience. Given the complexity of the material they are dealing with, starting with a simple selectionist framework could be a wise choice. But it does make Fernando and Szathmáry's understanding of what should be included in an Extended Synthesis rather different from that of most other contributors.

Given the different views that have been expressed about the reality, necessity, and coherence of the Extended Synthesis, there is clearly room for philosophers to weigh in on the matter. The final section brings two philosophers of science to the stage to discuss the very idea of an Extended Synthesis. Alan Love, who has written extensively and insightfully on conceptual issues in evolutionary developmental biology, homes in on the structure of the Extended Synthesis. Love argues that we should try to keep debates about content and structure separate. The other discussions in the book focus mostly on aspects of the content of the Extended Synthesis. Those who do attempt to say something about its structure—like the editors with their diagram of concentric circles—tend to mix in the content. But the structure of an Extended Synthesis should not fix its content, and it should be possible to reassess and revise structure and content largely independently.

Love suggests that it is helpful to think of extended evolutionary theory as having an *erotetic* (pertaining to questioning) structure. As being composed of 'problem agendas' around which a multitude of different subdisciplines of biology coalesce. Problem agendas are stable, because they address relatively robust research questions, even though there may be profound disagreement among its contributors about how these questions should be answered. Because of their focus on complex phenomena that do not respect disciplinary boundaries, erotetic units are especially useful for studying interdisciplinary interactions. In other work, Love has shown how it can be useful to think of evolutionary novelty as a problem agenda that invites multidisciplinary input (Love 2008; Brigandt and Love 2010). Love's suggestion to think about the evolutionary theory as a whole as having an erotetic structure is less illuminating. It leads him to sketch the structure of evolutionary theory as a web with thirteen problem agendas, interconnected via twenty lines of different shades. Among the problem agendas included in this web are ones familiar from the Modern Synthesis, like 'speciation' and 'adaptation', as well as relative newcomers like 'evolvability' and 'innovation and novelty'. But what to think of other problem agendas, like 'form and function'? Is this a distinct problem agenda? Or take 'variation', which sits at one end of the web, and 'diversity', which is located in the opposite corner. Are these distinct problem agendas? For multilevel

selection theorists they are surely part of a single problem agenda. Of course, this problem could be 'solved' by linking them up by drawing another line, but it is unclear what we gain from that. More generally, I am skeptical about Love's hope that erotetic structure of evolutionary theory "assists attempts to recover coherence through the vehicle of an Extended Synthesis" (ES, p. 434). Do we really need 'to recover coherence' with an overarching account of what is (should?) and what is not (should not?) be included in an Extended Synthesis?

In the final chapter, Werner Callebaut responds more skeptically to the call for an Extended Synthesis. He adds sociological and historical reflections in the mix, which lead him to propose a "dialectical solution" (p. 443). In contrast to Love's bottom-up analysis of the components of a synthesis, Callebaut takes a complementary top-down approach, touching on questions about the nature of unification more generally. Callebaut sees unifying and disunifying tendencies as necessary opposites for any science to make progress. Hence, debates about what should and should not be included in an Extended Synthesis can go on forever. Back in the 1940s and now, the extensions of the synthesis are negotiable, and "we are in the midst of this negotiation." (p. 458).

However, it seems to me that the current negotiation seems to unfold rather differently than the one that took place more than half a century to go. As Provine and others have observed (and as Callebaut recounts) the architects of the Modern Synthesis rather unambiguously made the synthesis "a vast cut-down of variables considered important in the evolutionary process" (Provine 1992, 176). Therefore, Provine suggests that the term 'evolutionary constriction' is a fitting description of what happened to evolutionary biology. In the 1930s and early 1940s, workers from different subdisciplines came to agree on a set of variables that play a role in the evolutionary process. This allowed them to set up opponents whose work they could contrast with their own. Think of Osborn on orthogenesis, or De Vries and Goldschmidt on saltational speciation. It is often forgotten that there was much disagreement among the architects, who all complained that their work had not received the exposure it deserved *within* the Modern Synthesis. Nevertheless, they formed a community by agreeing on who did not belong in their camp. The same goes for the 1980s, when Gould and his collaborators set up a different set of opponents. Thus, in the 1940s as well as in the 1980s, unity was in part the result of shared recognition of an out-group.

In comparison, the current talk about the Extended Synthesis appears to be on the opposite end of the spectrum of negotiation. Continuity with the Modern Synthesis is emphasized, and illustrated by welcoming one its few pluralistic architects as a friend. Even though Huxley was a tinge too 'adaptationist' to the editor's taste, they praise him for his openminded outlook. An outlook that is shared by them, and by most of the contributors to *Evolution—The Extended Synthesis*. But how to determine how far this pluralism should extend, without setting up new targets? How far should the lateral and vertical extensions reach? And without enemies, what creates the unity among this diversity? The diversity of contributions to *Evolution—The Extended Synthesis* was pragmatically restricted by the size of the table in the workshop room at the Konrad Lorenz Institute. But looking beyond that

workshop, what limits the number of seats at the High Table of the Extended Synthesis?

No matter what the prospects are for renewed synthesis, the essays in this collection are worth reading alone for being valuable extensions to what we know. Although the level and depth of the essays varies considerably, *Evolution—The Extended Synthesis* has much to offer for many audiences. To biologists and advanced students it offers a sneak preview at the diversity of exciting developments in evolutionary biology, some of which will be real eye-openers to those who have been out of touch with evolutionary theory for a while, or think of evolutionary biology as nothing but population genetics. For philosophers of biology, this collection will be an important resource for learning about recent developments in developmental biology and evolutionary genomics, and the complex conceptual issues they introduce.

(Re-)reading *Evolution: The Modern Synthesis* is certainly worth the effort as well, if only to realize how much our empirical and theoretical knowledge has advanced in the last 70 years. But more than that, Huxley's book is also a true *companion* volume for its laudable pluralistic tone, which resonates that of *Evolution—The Extended Synthesis*. Their shared outlook is reflected well by the following quotation:

> The nature of an organism influences the mode of its evolution. This applies at every level. Within the individual, the microscopic machinery of genes and chromosomes, the mode of cellular aggregation and tissue-growth; at the individual level, the type of reproduction, the way of life, the level of behavior, the method of development; beyond the individual, the size and structure of the group of which the individual is a unit, and its relations with other groups—all these, and many facts besides, have their evolutionary effects.

The words would not have been out of place as an opening paragraph in the introduction of *Evolution—The Extended Synthesis*. But Huxley already wrote these lines in *Evolution: The Modern Synthesis* (MS, p. 127).

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