Discussion

Lindsay Craig—The So-Called Extended Synthesis and Population Genetics (Biological Theory 5: 117–123, 2010)

Extended Synthesis: Theory Expansion or Alternative?

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In her critical essay on the Extended Synthesis in evolutionary theory, Craig (2010) argues that the concepts currently highlighted by EvoDevo represent significant and even insurmountable challenges to population genetics and, hence, to the core theoretical basis of the Modern Synthesis. Therefore she concludes that the ongoing conceptual developments in evolutionary biology are not appropriately described as an extension to the Modern Synthesis framework but represent a more substantial form of theory change.

Craig's position falls squarely into one of the three kinds of reactions we received concerning our edited volume (Pigliucci and Müller 2010) and the usage of the term Extended Synthesis. A frequent reaction is agreement with our main argument that evolutionary theory has significantly changed under the influence of new concepts emerging from multiple fields of evolutionary study, accepting our contention that population genetics has a valid part in the newly emerging framework, but that the additional models and concepts expand both the formal structure and the explanatory content of the Modern Synthesis. Disagreement with our position comes in two categories. One is the (more frequent) view that the conventional theory already covers all significant parameters of evolution and, therefore, nothing substantially new can have happened in evolutionary theory. Representatives of this view fervently argue that no change in the traditional framework is required and, hence, any talk of "extension" is superfluous (e.g., Hall 2000; Coyne in Pennisi 2008 and in Whitfield 2008; Minelli 2010). The second group of dissenters, including e.g., William Provine, a highly respected historian of the Modern Synthesis who felt strongly that our project was not radical enough (personal communication, December 2008), argue the opposite: the present challenges to the received theory are so substantial that no reconciliation with the classical framework is at all possible. Advocates of this view find themselves forced to contend that the Modern Synthesis needs to be supplanted by a new theory, and some propose in line with Craig that EvoDevo provides the kind of theory that could achieve this. We wish to make a brief comment on each of these two views.

The nothing-substantially-new position is the more surprising one. It effectively argues that seven decades of advancement in biological research have left no trace on a theory coined in the 1930s and 1940s. Even some firm supporters of EvoDevo deny that its conceptual consequences could in any way represent a challenge to the Modern Synthesis paradigm (Hall 2000; Minelli 2010). In an unlikely association, they are assisted by the die-hard population geneticists like Jerry Coyne and Michael Lynch (e.g., Lynch 2007; see Pigliucci 2008), who either dismiss new ideas about evolvability, robustness, modularity, and the like or—without a trace of detecting the inherent self-contradiction—dismiss those same ideas as straightforward derivations from the Modern Synthesis. Clearly, both criticisms cannot be on target simultaneously, and the skeptics here have the onus of seriously engaging the now substantial literature on evolvability and related concepts if they wish to deny its validity. Science does not make progress via armchair dismissal.

The more-change-is-needed position defended by Craig and others has a number of points in its favor. In fact, several of our colleagues would agree that some of the new concepts

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included in the Extended Synthesis contain aspects that go beyond a strictly Modern Synthesis explanation. Think of epigenetic inheritance, non-gradualistic modes of change, multilevel selection, or non-adaptive forms of character generation. However, does the inclusion of factors that permit different forms of organismal change justify a complete rejection of the earlier model? Craig's argument is strongly focused on EvoDevo. She more or less equates the conceptual changes afforded by EvoDevo with the Extended Synthesis and goes on to argue that the new framework cannot properly be called an extension because of the difficulties that may arise for population genetics to account for certain EvoDevo phenomena. Her worry that the challenges for the classical framework are insurmountable seems driven by a contention that all new evolutionary concepts, in particular the ones provided by EvoDevo (such as heterochrony, constraint, modularity, and evolvability), need to be accommodated by population genetics.

To begin with, it should be pointed out that EvoDevo is by no means the only subject field from which new theoretical advances have emerged, and our volume includes several sections that present conceptual developments in non-EvoDevo areas, such as genome evolution, multilevel selection, niche construction, and more. Besides these omissions in Craig's argument, it is not at all clear where the "insurmountable" difficulties for population genetics posed by EvoDevo would actually lie. Evolvability, for example, is an approach through which EvoDevo effects, such as modularity, can be integrated with the received formalism (Wagner and Altenberg 1996; Hendrikse et al. 2007). It is true that the population data of developmental character variation are largely lacking, but this is not an obstacle in principle, and a number of works already begin to address these issues (Hendrikse et al. 2007; Klingenberg 2010). Most importantly, it is not at all evident that the goal in evolutionary theory necessarily is to arrive at a full population-genetic explanation of the phenomena of evolving complexity. Based on Lewontin (1974) and others, Craig herself argues that the explanatory goal of population genetics is of no use in elucidating the evolution of phenotypic complexity, and we would add the stronger statement that an account of phenotypic evolution in general is simply not within the purview of population genetics (which deals with modes of genetic change). Why then demand that phenotypic complexity needs to be accommodated by population-genetic theory? Mounting the challenge to the Modern Synthesis in that way one seriously risks attacking a straw man.

Theories evolve. We take theories as families of models (Giere 1988) that pertain to the same natural phenomena. Different models can coexist within a larger theoretical framework as long as they don't contradict or invalidate each other. This is the case with the present state of evolutionary theory, in which population-genetic models, gene regulatory models, complex system models, developmental models, and others address different levels of evolutionary organization as well as different aspects of the multifaceted process of evolution (which, after all, is not just "a change in gene frequency" as standard population genetics textbooks would have it). EvoDevo by itself cannot represent an alternative to the classical paradigm because it has no independent theory of heredity and population dynamics. Hence, we feel that the inclusive and more pluralistic evolutionary framework proposed by us and our colleagues is best characterized as an expansion of the Modern Synthesis. This does not mean that nothing substantial has happened or that the conceptual additions represent only slight adjustments. Rather to the contrary, these additions are interpreted by us as major alterations in the structure of the evolutionary argument and have led to shifts of relative importance of some of the classical factors (Müller 2007; Pigliucci and Müller 2010). The new framework does not represent a formalized unification, just in the same way the Modern Synthesis was no unification of this kind. We now possess a more pluralistic theory, recognizing more factors and interactions than included in the classical model and with expanded explanatory capacity. We regard the term Extended Synthesis as a valid description of this state of evolutionary theory.

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