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COMMENTARY

Three Modes of Evolution by Natural Selection and Drift: A New or an Extended Evolutionary Synthesis?

Marion Blute[1]

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Abstract According to sources both in print and at a recent meeting, evolutionary theory is currently undergoing change which some would characterize as a New Synthesis, and others as an Extended Synthesis. This article argues that the important changes involve recognizing that there are three means by which evolutionary change can be initiated (genetically, ecologically, and developmentally) and three corresponding modes of evolutionary drift. It compares the three and goes on to discuss the scale of innovation and extended or inclusive and Lamarckian inheritance. It concludes from these that "new trends in evolutionary biology" are in part a new, and in part an extended evolutionary synthesis.

Keywords Evolutionary drift · Extended evolutionary synthesis · Extended inheritance · Lamarckian inheritance · Lamarckian evolution · New evolutionary synthesis

Introduction

According to many, evolutionary theory is in something of a turmoil, which has been building slowly over the past quarter century or so (for one overview see Griffiths and Stotz 2013, Chap. 8) and which culminated perhaps in Laland et al.'s "Does evolutionary theory need a rethink? Yes, urgently" (2014) and the reply by Wray et al. "No, all is well" (2014). These papers eventually resulted in a discussion meeting on "New Trends in Evolutionary Biology: Biological, Philosophical and Social Science Perspectives" sponsored by the Royal Society and the British Academy, held at the Royal Society in London on November 7–9, 2016. A rough content analysis of the abstracts (available online at the Royal Society 2016) for that meeting reveals that about two-thirds of the speakers tilt towards a new rather than an extended evolutionary synthesis.[1] That impression was confirmed by informal observation at the meeting itself. The participants from either group may not, however, have been statistically representative of evolutionary biologists as a whole who would probably prefer to hew more closely to the traditional synthesis. Interestingly one of the more revealing comments made from the floor was not the classic "It isn't true, it isn't new, we knew it all along," but one which negated the first part of that but maintained the other two parts, claiming in effect, "It is true, but it isn't new, we knew it all along."

Swirling about in this new or extended brew is a proliferation of concepts pertaining to evolution—older ones such as the Baldwin effect (1896), Waddington's

✉ Marion Blute
marion.blute@utoronto.ca

[1] Department of Sociology, University of Toronto, Toronto, ON, Canada

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[1] Numbering all of the entries available online (Royal Society 2016) from 1 to 24 in order, one is missing an abstract and two others are roundtables (numbers 12, 16, and 24) leaving 21 abstracts. Those 21 abstracts are almost evenly divided between those that say nothing directly on the new or extended question (nine abstracts—numbers 3, 5, 9, 10, 15, 17, 18, 19, and 21) and those that express some direct opinion (12 abstracts—numbers 1, 2, 4, 6, 7, 8, 11, 13, 14, 20, 22, and 23). Of the 12 that express some direct opinion, two managed to stay right on the midline (numbers 1 and 22), seven are on the new side (numbers 6, 7, 8, 11, 13, 14, and 23) and three are on the extended side (2, 4, and 20). However, examining the rest of the content of the abstracts summarizing what the authors actually planned to say in the talks, of the nine who express no direct opinion, it is obvious that seven of them are on the new side as well (numbers 3, 5, 9, 10, 15, 18, and 21) while only two remain ambiguous (numbers 17 and 19) which makes for a total of 14/21 or two-thirds that think something major is afoot in "new trends in evolutionary biology."

Table 1 Three modes of evolution by natural selection and of drift

Mode	Genetically constructive	Ecologically (i) Selective or (ii) Inductive	Developmentally constructive
Leader of change	Genes New genes in an old env.	Ecology Old genes in a new env.	Development Old genes and env., new dev.
Sequence	geno → devo → eco → evo → geno	(i) eco → evo → geno (ii) eco → devo → evo → geno	devo → eco → evo → geno
Relationship between genetic and evolutionary change	Genetic change leads eventually to an evolutionary change	Evolutionary change leads to a genetic change	Evolutionary change leads to a genetic change
Relationship between developmental and ecological change	Developmental change leads to an ecological change	(ii) Ecological change leads to a developmental change	Developmental change leads to an ecological change
Evolutionary drift	Genetic drift	Ecological drift	Developmental drift

genetic assimilation (1953), Gould and Vrba's exaptations (1982), and Brakefield and Roskam's constraints (2006) of course, but also newer ones including EvoDevo (dealing with the interaction of evolution and development), EcoDevo (dealing with the interaction of ecology and development), and even EcoEvoDevo. The list is very long (and undoubtedly some have been missed) but includes adaptive mutation (Cairns et al. 1988), epigenetic inheritance and Lamarckism (Jablonka and Lamb 1995), the ontogeny of information and developmental systems (Oyama 2000), phenotypic plasticity (Pigliucci 2001), genetic accommodation (West-Eberhard 2003), developmental plasticity (West-Eberhard 2003), genes as leaders and followers (West-Eberhard 2003; Schwander and Leimar 2011), niche construction (Odling-Smee et al. 2003), biased embryos (Arthur 2004), facilitated variation (Kirschner and Gerhart 2005), four dimensions of evolution—genetic, epigenetic, behavioral, and symbolic (Jablonka and Lamb 2005), compositional evolution (Watson 2006), an extended evolutionary synthesis (Pigliucci 2007; Pigliucci and Müller 2010; Laland et al. 2015), a new definition of evolution by natural selection (Blute 2008, 2010), transformations of Lamarckism (Gissis and Jablonka 2011), developing scaffolds (Caporael et al. 2014), arrival of the fittest (Wagner 2014), evolution learning (Watson and Szathmáry 2016), and white knight traits (Wagner 2017). And then of course there is dual inheritance, cultural transmission and evolution, and gene-culture coevolution. "Many of them include echoes of the outsiders' criticism—that gradualist, random gene-centered evolution is unable, despite Dawkins' (1995) claim, to 'climb mount improbable.' At the risk of simplifying, they tend to think that the variation side of the 'variation and selection' theme (with the roots of variation in development) requires more elaboration if the introduction of novelty and the evolution of complexity are to come to be truly understood" (Blute 2010, p. 205).

This article attempts to boil down the novelty by arguing that there are three means by which evolutionary change can be initiated (genetically, ecologically, or developmentally), three corresponding modes of evolutionary drift, and compares them. It then discusses the scale of innovation and extended or inclusive and Lamarckian inheritance and arrives at the conclusion that "new trends in evolutionary biology" are in part a new and in part an extended evolutionary synthesis.

Three Modes of Initiation

Genetically Constructive

A new genetic mutation or recombination alters development in such a way that its carrier perceives, defines, or constructs its ecological environment differently. For example, it eats something that has been available but was previously uneaten by its ancestors and contemporary conspecifics. This results in an evolutionary change—the new variant survives and/or reproduces better or worse than others—and to further change in gene frequencies in the population. This case of "genes as leaders," i.e., new genes or gene combinations in an old environment, with selection acting in a "backward" direction, despite the inclusion of niche construction (Odling-Smee et al. 2003), is traditional—the causal sequence is geno → devo → eco → evo → geno (Table 1, column 1; Blute 2016 and references).

Ecologically Selective and Inductive

Also traditional is the ecologically selective case in which existing genetic variations in a population are changed in relative frequencies when the environment changes—say the latter becomes warmer or cooler—without changing the course of development of any of those variants: eco → evo → geno (Table 1, column 2, i). However, ecology can initiate evolutionary change in another less familiar way as well, inductively. A novel environmental influence on a phenotype such as a new food becoming available leads to a developmental change (it eats the new food), which leads to an evolutionary change (those who do survive and/or reproduce better or worse than others), which leads to a change in gene frequencies in the population. This is possible either because of other genes (Gould and Vrba's (1982) preadaptation or exaptation) or because the new inductive influence on development engages a previously unutilized part of the range of a plastic response. In such cases of "genes as followers" (West-Eberhard 2003; Schwander and Leimar 2011), i.e., old genes or gene combinations in a new environment with selection acting in a "forward" direction, the causal sequence is eco→devo→evo→geno (Table 1, column 2, ii; Blute 2016 and references).

Developmentally Constructive

There is a third mode as well, as many have argued, initiated by changes in "the developmental system." It has been the most difficult to think and talk about probably because we lack a general process theory of development. But if, for the sake of argument, we posit a theory of multicellular development as an encapsulated or nested evolutionary process among cells in Metazoa or among meristems in plants (as many have, e.g., Buss 1987; Kupiec 2009; Blute 2010; Clark 2011) then a change might originate not from a new genetic mutation or recombination, nor from a new inducing ecological environment, but from within development. A novel somatic mutation or cellular epigenetic change, cellular induction, or cell selection event, for example, could affect, again for better or worse on the more aggregate multicellular organismic level, how the latter constructs its environment—e.g., like the genetically constructive, eating something that has been available but was previously uneaten by its ancestors and contemporary conspecifics. The sequence would be devo → eco → evo → geno, i.e., similar to the ecologically inductive in the sense that the heritable effect is made possible by other genes or because a previously unexplored range of a plastic response has been engaged but with the place of eco and devo switched (Table 1, column 3).

Comparisons

There is a long history of disagreement, even confusion, related to the "units of selection problem" about whether evolution is a matter of differential survival and/or reproduction of organisms in a population or a change in gene frequencies in a population. "For example, one widely read textbook refers to evolution as 'changes in the properties of groups of organisms over the course of generations' (Futuyma 2005), whereas another defines it as 'changes in allele frequencies over time' (Freeman and Herron 2007)" (Losos 2014, p. 4). Note that in the three modes above both are included but are separated. In all cases, an evolutionary change leads to a genetic change, but in the genetically constructive case, the sequence is initiated by an earlier genetic change. Additionally with respect to development and ecology, in the genetically and developmentally constructive cases, a developmental change leads to an ecological change; while in the ecologically inductive case, an ecological change leads to a developmental change. So there are three means by which evolution can be initiated, each with distinct sequences of events (two in the ecological case depending upon whether events begin with existing or with new genetic variation). Together they constitute a unified theory of evolution by natural selection that includes not only evolution and genetics, as do traditional descriptions of the evolutionary process, but also development and ecology. In varying cases geno, eco, or devo initiate change but never evo—naturally enough because that is what we are trying to explain!

Evolutionary Drift

If there are three modes of evolution by natural selection, then there are three modes of drift (sampling error in finite populations) as well—the genetic, the ecological, and the developmental. The genetic is well established, but consider the ecological. Herbivores grazing on vegetation would typically face slightly differing ecological conditions—some patches would contain a little more moisture than others, some receive a little more sun than others, and hence some patches of vegetation would be a little greener and thicker than others and so on. Hence, in a finite population of patches, rare slightly-more-favorable ecological conditions could be lost, or rare slightly-less-favorable ecological conditions could be retained—solely on the basis of chance alone. Similarly, novel developmental events are unlikely to be identical for all, and thus in a finite population of developments, there too drift as well as selection could play a role in population-level developmental outcomes. Therefore, given three modes of evolution by natural selection, the traditional genetic drift is only one of three modes of "evolutionary drift" (Table 1, last row).

Scale of Innovation and Extended and Lamarckian Inheritance

Although some saltationists both preceded and came after them, both Lamarck and Darwin were gradualists. However, since Fisher, the Modern Synthesis has largely maintained that most evolutionary change has involved many loci or genes, each of a small effect, rather than one or a few, each of large effect. This has been challenged from time to time including in modern times (e.g., Bell 2009; Chouard 2010) but the challenge has been controversial as well (e.g., Wellenreuther and Hansson 2016), and there does not seem to be any clear answer to this question. Consider something as simple as human height, which is highly heritable. While genome-wide association studies have identified some 700 common variants affecting human height, a recent Exome chip study revealed 83 low-frequency variants with effects of up to 2 cm, greater than ten times the average effect of common variants (Marouli et al. 2017). Probably the best tentative conclusion to draw for now is that both are possible—evolutionary innovation can involve both tortoises and hares. And if that is the case for the genetic mode, it may well be the case for the ecological and developmental ones as well, as some have argued (e.g., Newman and Bhat 2011).

The modern evolutionary synthesis also more or less exclusively confined itself to genetic inheritance, but what is inherited extends far beyond that. There are three broad categories of inheritance beyond genes—the non-genetic but still included in reproductive cells, that which is not confined to reproductive cells but is still confined to the organism (for example lactation in mammals or other forms of parental care), and that which extends beyond the organism (niche constructions that last beyond a single life cycle). There is a good reason why, despite its small proportion of the cell by dry weight, so much inheritance has come to be mediated genetically. The gene's basically digital nature facilitates stability in transmission, by contrast with the analog, which is subject to cumulative degradation of information (Dawkins 1995)—the same reason why our devices have come to receive, store, and transmit information digitally.

Nevertheless, extended inheritance is common, so "inherited" could be substituted for genetic in Table 1. Of course extended inheritance is not necessarily Lamarckian inheritance (the inheritance of acquired characteristics). Extended inheritances themselves may be inherited or be newly acquired. Nevertheless, Lamarckian inheritance is also common. An example I like to use is a parental cell doubling in size and dividing once. Then half of the material inherited by offspring was acquired by the parental cell rather than inherited by it—in that simple case Lamarckian inheritance is 50% (Blute 2010, p. 205). One question about extended inheritances that are Lamarckian, i.e., acquired, is why they exist at all. Leaving aside the question of sexual reproduction, why (in the absence of mutation broadly understood) do not organisms always "replicate" in all respects, including those that extend beyond the genome? The answer is that "life cycles" evolved by selection can be more than one generation long—for example, under crowding one common strategy is the production not of more offspring, but of fewer higher quality ones (by eukaryotic cells engaging in autophagy, for example), offspring that produce their own offspring, i.e., grandoffspring. A more extreme example is some parasites that cycle through a whole series of generations and forms. But "cycling" here is the operative word. It also should be emphasized that Lamarckian inheritance does not equate with Lamarckian evolution—understood as the preferential acquisition and inheritance of acquired adaptations. So those few who spoke from the floor at the meeting in favor of a reintroduction of "intentionality" into evolutionary theory were wrong in my opinion, unless of course intentionality was meant in the limited sense of evolved adaptive phenotypic plasticity. It is well understood by evolutionists that uncertainty favors bet-hedging (Roff 2002, Chap. 5), and uncertainty with reliable cues favors adaptive phenotypic plasticity (Roff 2002, Chap. 6). Presumably these could evolve by any of the modes of evolution by natural selection.

Conclusion

So are we in the midst of the emergence of a new or an extended evolutionary synthesis—revolution or evolution, radical or moderate change? On the radical side, the Modern Synthesis embodied in population genetics largely viewed evolutionary change in a lineage as beginning with a new genetic mutation or recombination or existing genetic variation. Recognizing explicitly three, rather than a single mode of initiation, and three modes of drift, as well as the ubiquity of extended and even of Lamarckian inheritance appears indeed to be a New Synthesis. On the conservative side on the other hand, while recognizing that heredity, ecology, or development can be the prime mover in any particular case of evolutionary change, in none of the three should such initial events be statistically biased in the direction required for them to be adaptive. Examples of the opposite to the contrary, they are (and are probably more) likely to be maladaptive than adaptive. It has become common to use biological evolution as a model for understanding cultural evolution, but the analogy can be drawn in reverse as well. And in the social sciences the evidence has long been clear that innovations are not statistically biased in the direction required for them to spread further. That is the case most obviously for stock picking and market timing, but the evidence has long been available in less obvious cases—papers being cited, patents being utilized, new businesses being founded, and new products being successfully marketed, for example (Blute 1979). If Lamarckian evolution is not true in the human cultural realm, it is surely even less likely to be so in the biological one. As Donald Campbell always insisted, evolutionary novelties (and I would add the three kinds of evolutionary novelties) are not prescient. After all, how could it be otherwise? It would be a miracle. In any event, whatever one's views on these matters are, a major and diversified research project is underway on the extended evolutionary synthesis (see http://extendedevolutionarysynthesis.com/) and all evolutionists should watch the results with interest.

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