Essay Review

Down with Natural Selection?*

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ABSTRACT Biologists are increasingly reexamining the conceptual structure of evolutionary theory, which dates back to the so-called Modern Synthesis of the 1930s and 1940s. Calls for an Extended Evolutionary Synthesis (EES) cite a number of empirical and theoretical advances that need to be accounted for, including evolvability, evolutionary novelties, capacitors of phenotypic evolution, developmental plasticity, and phenotypic attractors. In *Biological Emergences*, however, Robert Reid outlines a theory of evolution in which natural selection plays no role or—worse—actually impedes evolution by what Reid calls "natural experimentation." For Reid, biological complexity emerges because of intrinsic mechanisms that work in opposition to natural selection, a view that would reopen old questions of orthogenesis and Lamarckism. This review outlines why we do need an EES, but also why it is unlikely to take the shape that Reid advocates.

THERE IS MUCH TALK these days of the possibility that the Modern Synthesis, the current conceptual framework in evolutionary biology, is due for a makeover (Müller 2007; Pigliucci 2007a). This is ruffling quite a few feathers, though it should not really be surprising that a theory proposed in the 1930s and 1940s—before the discovery of the structure of DNA, not to mention genomics and evo-devo—may be a bit out of date. The question, however, is what, exactly,

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an Extended Evolutionary Synthesis (EES) would look like, and here is where the current discussion can be both intense and confusing. This, too, of course, should not come as a shock, as historically any major change in scientific theorizing has been accompanied by turmoil and disagreement. The key is to clear the air from unhelpful notions and look for the tasty meat where the smoke came from.

Biological Emergences by Robert Reid is an interesting contribution to the ongoing debate on the status of evolutionary theory, but it is hard to separate the good stuff from the more dubious claims. Reid seems to be somewhat ambivalent about what role, if any, natural selection will have in the new theory. In some instances he makes the extraordinary claim that natural selection does not have causal power, only to tell us a few lines later that it is actually a barrier to evolution (hence, it does have consequences), and in yet other places he says that the concept of natural selection will be an integral, albeit minor (but still, one would think, causal), component of the new synthesis. It is difficult to reconcile these different views of natural selection. Even if selection affects only "fluctuations in the demographics and ecology of populations" (which, rather strangely, Reid calls "non-evolutionary" [p. 401]), how does it follow that "natural selection is no longer considered to have any causal validity for evolution" (p. 405)? Reid advises us to "get rid of the expressions 'natural selection' and 'selection pressure' altogether" (p. 405) because the latter is "a metaphorical external agent" (p. 393), a novel concept that will surely provide philosophers of science with a field day. (An agent cannot be metaphorical, because it would not have causal powers, and therefore would not be an agent.)

Reid's main argument is that natural selection is insufficient (or irrelevant, or an obstacle) to account for evolutionary change, especially the kind of change that has been hardest to explain so far: the evolution of complex structures and novel functions or features. I would agree, and so do authors ranging from Stuart Kauffman (1993) to Mary Jane West-Eberhard (2003) to Gerd Müller and Stuart Newman (2003). The additional (or alternative, depending on the case) explanatory principles offered by various authors to account for phenotypic evolution include attractors in phenotypic space as conceptualized by complexity theorists like Kauffman, the role of developmental phenotypic plasticity in catalyzing change ahead of genetic modifications (West-Eberhard's "genetic accommodation"), the evolution of evolvability, the existence of epigenetic inheritance systems, and the discovery of "capacitors" of phenotypic evolution, to mention a few of the main candidates (Jablonka and Lamb 2005; Pigliucci 2007b; Rutherford and Lindquist 1998; Wagner and Altenberg 1996).

The possibility of the insufficiency of natural selection as an explanatory principle for the biological sciences is a pretty big deal, and if eventually accepted by the evolutionary community would represent a change in the basic Darwinian framework that would go beyond the import of the Modern Synthesis itself. After all, the Modern Synthesis did not question the sufficiency of common descent and natural selection, the two pillars of Darwin's contribution. What happened during the 1930s and 1940s was a reconciliation of Darwinism with the emergent science of genetics, a reconciliation that was engineered largely on the basis of empirical and theoretical work in population genetics. The result was a theory that provides an excellent account of how gene frequencies change within populations as a result of selection, mutation, recombination, migration, and drift (stochastic variance). As many people have acknowledged, though, the Modern Synthesis left out developmental biology (hence the now not-so-recent excitement about so-called evo-devo; Love 2003). Less well understood is the equally puzzling fact that the Modern Synthesis basically ignored ecology (despite a strong research program in evolutionary ecology), so much so that ecologists and evolutionary biologists now hardly talk to each other, and we have no organic theory of how community and ecosystems ecology are connected to evolutionary biology.

All of this is exciting enough, but to call for an outright rejection of natural selection, as Reid does, takes guts. Is it justified? Reid certainly thinks so, and the reader gets a taste of the strength of his conviction early on in the book. On p. 61 he begins a section with the provocative title of "Religious Fervor." In it we learn that "paradigms [such as the Modern Synthesis] whose popularity is underpinned by polemic, consensus, and belief have a lot in common with religion." He goes on, referring to some of the main architects of the current paradigm in evolutionary biology in outright derisive terms: "ultra-Darwinism only demanded an exorcism of demons. . . . Its roots go all the way back through molecular reductionism, selfish-gene-ism, the Williams purge . . . to the Biblical language of *The Origin of Species*." Ouch. The man has passion, and I find myself agreeing with him that what philosophers call "greedy" reductionism, gene-centrism, and the early rejection of group selection (the "Williams purge") are in fact excesses to be corrected by a more ample view of evolutionary phenomena and their causes. Still, perhaps because I have experienced true religious fervor in battling with creationists and intelligent design proponents for the past decade, I simply cannot see Richard Dawkins as "the Martin Luther of biology" (as Reid labels him, quoting Steve Jones). I do not shy away from frank intellectual confrontation, but I do not think it serves anyone's purpose (expect, perhaps, the above mentioned creationists) to hurl insults at one's intellectual foes.

Choice of tone aside, some of Reid's proposals are questionable in their substance. He claims that what he calls "natural experiments" arising out of emergence are the real stuff of evolution, and that the latter is an inherently progressive process. Now, the word *emergence* has gathered an unfortunate reputation among some biologists, and their distaste for it will not be helped by Reid's book. This is too bad, because there is nothing mystical about emergence, and the concept will in fact be very useful in shaping an EES. At its most basic, emergence is what happens whenever "the whole is more than the sum of its parts" (another phrase used by Reid, and one that is also guaranteed to raise eyebrows in certain quarters), or in other words, whenever one has interactions among parts of a system. A simple example is provided by water: as we all know, water is a molecule made of two atoms of hydrogen and one of oxygen; yet, one would be hard pressed to predict the macroscopic qualities of water (freezing and boiling point, density/temperature relationship, etc.) by somehow averaging out or summing up the individual properties of hydrogen and oxygen. There is no magic here: the emergence of those macroscopic qualities is the result of the fact that water has a particular tridimensional structure that allows molecules to bond in a certain way, and it is that nonlinear interaction that explains the macroscopic properties of the compound.

Emergence is a ubiquitous characteristic of life, seen in countless systems from the eukaryotic cell that arose through a combination of symbionts, to multicellular organisms and their ability to specialize groups of cells for specific functions, to animal societies, to the structure and properties of communities and ecosystems. Emergence is also a concept that simply doesn't enter into the Modern Synthesis, no matter how much hand waving its supporters may wish to engage in. Emergence, in turn, is currently best understood within the conceptual framework of complexity theory (think of the complex patterns typical of the aptly named game "Life," arising out of a simple set of rules controlling the local behavior of individual elements in the game). Complexity theory, again, is something that simply did not exist at the time of the Modern Synthesis and that would have to be an integral part of a possible EES. What is unclear, however, is why incorporating emergence in evolutionary theory implies a rejection of natural selection, much less the resurrection of such dubious concepts as progress (and even orthogenesis and Lamarckism).

Let's take Reid's emphasis on progress in evolution as an example. *Progress* has had a long and controversial history in biology, from the Aristotelian and then medieval idea of a *scala naturae* on to Stephen Gould's account of increasing complexity as a "left wall effect," where organisms got more complex over time because, well, they started simple and there was only one way to go! Reid makes progressive evolution a major part of the thrust of his book, and he even uses it to conclude that "Lamarck was not altogether wrong in his progressionism" (p. 406). Yet, we have to wait until almost the end of the book, in chapter 11, to find an explicit, if too brief, definition of what he means by progress: "by progressive evolution I mean increase in complexity. And complexity is not simply a multiplicity of parts, but an effective ordering of the parts through self-organization" (p. 406). We have, then, two interrelated concepts here: progress and complexity. I doubt any biologist in his right mind would deny either that (biological) complexity is characterized by "an effective ordering of parts" (in other words, it is not just a random pile of stuff), or that evolution has seen an increase in biological complexity, pretty much regardless of how one measures complexity. The controversial parts of Reid's idea are that structured complexity arose from self-organization (as opposed to natural selection), and that there is some (vague) sense in which this was bound to happen (hence the reference to Lamarck).

I think Reid is half right on the first point and probably wrong on the second. It is clear to me from work on complexity theory and in developmental biology that self-organization is here to stay: we simply cannot make sense of, say, the three-dimensional structure of proteins, not to mention tissue organization, without factoring in the capacity of proteins and cells to self-organize. Genes are certainly one component of the causal network, but they are equally surely not the only relevant one. We keep hearing of the successes of genomics, but few people point out the obvious: its glaring failures. Just a few years ago enthusiasts of genetic reductionism predicted that once we knew the sequence of genes in humans we would solve all sorts of theoretical and practical problems in human biology. But as soon as the human genome rush was over, we started hearing insistent calls for additional "omics"—because, you see, if you don't also account for the (emergent) properties of proteins, metabolism, physiology, and development, well, it turns out you don't go very far. But "effective ordering of parts" doesn't mean just nonrandom assembling, it means adaptive assembling. When I generate complex forms and behaviors on my computer screen while running the complexity theory-inspired game "Life," I get nonrandom complexity, but it isn't "effective" because there is no fitness measure. As far as I can fathom, we need the concept of natural selection to bring fitness into the equation, so that self-organization has to dance a tango with natural selection for adaptive complexity to come about. (Although Reid is correct when he claims, equally, that natural selection has to dance with emergence if we want to get the kind of complexity that characterizes the biological world.) To put it in another fashion: selection without emergence would probably produce only very limited and simple structures, while emergence without selection could not account for the "fit" between organisms and their environment that so impressed intelligent design proponent William Paley and for which Darwin sought a naturalistic explanation.

As for some Lamarck-style sense in which adaptive emergent complexity was inevitable, or even particularly likely, this is a metaphysical statement at best and quite dubious even on philosophical grounds. When Reid says, for instance, that "symbioses were major emergences en route to the origin of eukaryotes," he is likely right in the sense that the eukaryotic cell probably would not have originated without symbiotic events bringing together simpler elements. But there is an evolutionary route to be seen only in the retrodictive historical sense: it is quite easy to imagine a planet where symbiosis never occurred and life never got to eukaryotes at all, pace Lamarck and his intellectual descendants. Of course, there is a long tradition in biology of arguing about the inevitability (or not) of certain evolutionary outcomes: Gould and Dawkins spilled quite a bit of ink discussing what would happen if one could rewind and replay "the tape of life"

(Sterelny 2001). But there is no tape of life, and we have no idea of the likelihood of alternative outcomes of early evolution. It may very well be that intelligent, self-aware bipeds were inevitable (as Dawkins maintains), or it may be that a planet perennially populated by boring bacteria was avoided only by a highly unlikely sequence of events (as Gould claims). We don't know, and I don't see the point of arguing one way or the other.

Reid, for all his despising of what he terms "nothing-but reductionists" (as in "nothing but genes"), also rightly warns us about the perils of going too far on the other side and embracing "the romantic extreme of transcendental holism, which celebrates complexity for its mystery" (p. 431). It is therefore unfortunate that, just a few paragraphs before, he praises James Lovelock's idea of the earth as a super-organism (the so-called "Gaia hypothesis"), chastising Dawkins for dismissing Gaia on the grounds that it couldn't evolve because "it has never been in competition with others of its type." I think Dawkins gets it exactly right here (Pigliucci 2005), and in fact this is a perfect example of where one should draw the distinction between emergence and natural selection and their respective roles in evolution. I have no doubt that the earth's biosphere (please, let us drop silly anthropomorphisms rooted in ancient Greek mythology) is, in fact, an emergent property of the physico-chemical-biological interactions that underlie it. But it did not evolve in any biological sense of the word, unless by *evolution* we simply mean change over time. Our biosphere is complex, but not in an adaptive manner, because there has never been natural selection acting on it as a whole and the concept of fitness simply does not apply. Similarly, hurricanes are highly complex, emergent structures, but I doubt even Reid would go as far as claiming that they are examples of evolution.

I have focused most of this review on the disagreements I have with Reid, because that is where the matter for further discussion is likely to originate. There is, however, quite a bit to commend in the book in terms of Reid's challenge to "ultra-Darwinism," and what makes this a valuable effort is the fact that it is not an isolated incident: more and more scientists are playing with the same pieces of the puzzle that appear in Reid's book (and additional ones as well), though they may be arranging them in different fashions. It is becoming increasingly clear that we are moving toward a new synthesis in evolutionary biology and are forging a general idea of what it might look like, though we are not quite there yet. Throughout the book Reid complains that biological theory has been highjacked by an obsession with quantitation (an instance of physics envy), while what we need most of all is a theory of qualitative change: "quantitative rigor has become an end in itself . . . but it is anti-intellectual if cases where it is not as easily applied are dismissed as 'tiny and uninteresting'" (p. 433). It is this sense that biologists need in order to reclaim their proper theoretical domain and set of intellectual tools that will bring biology into its own mature phase, likely during the 21st century.

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