Acta Biotheor (2008) 56:249–255
DOI 10.1007/s10441-008-9051-z

BOOK REVIEW

Evolution Despite Natural Selection? Emergence Theory and the Ever Elusive Link Between Adaptation and Adaptability

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Published online: 26 March 2008

A review of Robert R.G. Reid, *Biological Emergences: Evolution by Natural Experiment*. 2007, MIT Press. Cambridge, MA. ISBN–10: 0-262-18257-2, 518 pages.

Does adaptability evolve in concert with adaptation or independently of it, emerging as a by-product of organismal existence regardless of the fitness consequences per se? Answering this question would resolve a number of paradoxes in evolutionary biology. In genomics, it would explain the evolution of networks that combine evolvability on long evolutionary scales with robustness during development, as well as the remarkable redundancy and dispensability of gene effects in sequenced genomes. In physiology and biochemistry, it would shed light on puzzling evolutionary transitions in homeostasis—a trait that should be resistant to all changes, and address the contrast between evolutionary stasis and rapid within-generation physiological and biochemical adjustments of organisms to their environments. And in behavioral biology, it would resolve the conflicting role of behavioral plasticity as "inhibitor" versus "driver" of evolutionary change. The reason for such importance is that the link between adaptation and adaptability enables us to envision the connection between the maintenance of adaptation and evolutionary change and between the generation and maintenance of novelties—two major goals of evolutionary theory (Williams 1966; Lewontin 1983).

Partially as a compensation for the deficiency of the generative processes in the neo-Darwinian evolutionary framework, and for the lack of clear links between these generative processes and the functional importance of traits, contemporary evolutionary theory overemphasizes natural selection as an active mechanism that "favors" a particular developmental variation while also subsequently sorting this variation. Robert G. B. Reid's thought provoking and authoritative new book—"*Biological Emergences: Evolution by Natural Experiment*"—seeks to reestablish

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the proper placement of generative processes in evolutionary theory, a placement that would not only explain the evolution of organismal complexity and adaptive divergence, but also establish the link between adaptation and adaptability. The book's main focus is emergence theory—the generation of stable novel structures that can amplify and replicate without differential fitness effects. The fundamental premise of this, as well as of the earlier book by the same author—"*Evolutionary Theory: The Unfinished synthesis*" (Reid 1985), is that the incompleteness of the neo-Darwinian evolutionary framework results from erroneous designation of natural selection as the cause of both adaptation and evolutionary change. The criticism of the selection-centered approach, the distinctions between the causes of adaptation and adaptability, and the exploration of the origin of evolutionary novelties are the main goals of the book, and in these goals the book makes its most important contributions. The author presents a comprehensive and uncommonly up to date, for a book of its size, treatment of emergence theory—from annotated eighteenth century correspondence to publications of the last 2 years—that by itself makes this book a unique contribution to any evolutionary biology library.

The book is not as effective in establishing biological emergence as a framework for evolutionary biology. The author decisively moves the generative cause of evolutionary change from selection to developmental variation, where it undoubtedly belongs, but he does not convincingly extend the links from this new position to other essential components of the evolutionary framework—most importantly, inheritance. Thus, whereas neo-Darwinian theory is rightly criticized for focusing on maintenance and stasis and ignoring generative processes and evolutionary change, here the pendulum swings to the opposite extreme by illuminating generative processes while giving only superficial attention to the details of their evolutionary retention. The author is clearly frustrated with the ease with which current empirical biology, having outgrown the straightjacket of the modern evolutionary synthesis, has moved on ignoring the synthesis' logical flaws, but nevertheless keeping the neo-Darwinian framework for popular media and undergraduate textbooks. This frustration sometimes results in missed opportunities to integrate different approaches or at least gain insights into persistence of the modern synthesis. In this review I will examine the author's arguments along with the reasons why alternative frameworks, such as emergence theory that is so eloquently and authoritatively reviewed in this book, are not more readily picked up to fill the current conceptual void in evolutionary theory.

1 Natural Selection in Evolution: Metaphorically Active but Mechanistically Passive

The book's most important contribution is a comprehensive critique of the selection-centered framework of modern evolutionary biology (first two chapters). The main premise in these chapters is that, although natural selection plays a central role in the maintenance of already evolved adaptations under prevalent conditions, acting as "the conservative ringmaster" assuring that the most beneficial organism-environment associations are preserved, it largely prevents evolutionary change per

se and thus plays only a small part in evolutionary diversification. Three main groups of arguments are advanced to support this thesis.

The first group of arguments challenges the primacy of selection in generating organismal novelty and complexity because: (i) selection cannot act on characters that are not yet in existence and thus cannot be invoked as the cause of novelty, (ii) function, including survival and reproduction, occurs prior to *differential* survival and thus fitness consequences of organismal forms are secondary to their origin, (iii) natural selection is expected to prevent evolutionary transitions between levels of organization, instead acting to protect, stabilize, and fine-tune organization at each level, and (iv) without channeling effects of development that result in discrete patterns of novel variation, natural selection cannot produce continuous trends of phenotypic expression, such as needed for linear exaggeration of complex structures, based only on random mutational input.

Second, it is the absence of natural selection that enables innovations and diversification in organismal forms—"natural experiments" as the author calls them. The examples of artificial selection and domestication, commonly invoked as proof of the creative role of selection, are used here to highlight the fact that innovations and diversifications of domestic animals and plants are not *created* by artificial selection. Instead shielding of organismal forms from predation and competition enables developmental expression of natural experimentation with novelties. This is a powerful reminder that programs in animal and plant breeding are just that—a sort of "mating service" with the goal of preserving unusual, novel, and exaggerated traits, not survivable under *natural* selection, but, crucially, arising prior to the preservation efforts (see also Oyama 2000). The author extends this argument to suggest that diversification and generation of novelties in the wild are often similarly accompanied by relaxation of natural selection, such as during ecological invasions or colonizations where reduced predation and competition leads to ecological release. Also instructive here is the commonly observed reversion of domestic varieties to a wild type under consistent natural environments.

Third, the author contrasts the speed with which organisms mount novel biochemical, physiological, and behavioral responses to changing environmental conditions within a generation with the slow pace of evolutionary change to suggest that evolutionary stasis is largely an outcome of efficient and constraining natural selection and not of the speed with which novelties can appear.

Such a wide-ranging critique of the role of natural selection in evolutionary change is important. As the author points out, unwarranted extension of natural selection from the original role of a passive post-production filter to an active and anticipatory agent that modifies organic forms (e.g., Eldredge 1985) essentially confounds evolution and natural selection. This makes evolutionary theory vulnerable to charges that natural selection must be a sufficient explanation for life's diversity and complexity (which it is not), or otherwise evolution should itself be rejected. More importantly it confuses the generative evolutionary forces with their effects and consequences (Schmalhausen 1938, 1969), and by overemphasizing maintenance of organismal forms, gets us farther from understanding their origins (Newman and Müller 2000; Müller and Newman 2003).

The critique of neo-Darwinism's selection-centered approach energizes many arguments in this book, sometimes at the cost of missed opportunities to examine why the neo-Darwinian framework is so persistent even in fields explicitly concerned with generative processes, such as evolutionary developmental biology. Under both emergence and neo-Darwinian theories, natural selection facilitates evolution of complexity by preserving, combining, and accumulating past adaptive structures and their complex developmental pathways (e.g., Chetverikov 1926, Wagner 2001; Wagner 2005. Change or relaxation of selection pressure on coadapted complex structures facilitates expression of previously hidden or novel phenotypic variation (e.g., Badyaev 2005). Population genetic theory provides formal predictions about the pattern and extent of developmental variation expressed when composite adaptations experience novel environmental pressures, in relation to structure's modularity, genetic, functional, and developmental integration, and the history of past selection (Cheverud 1996; Wagner and Altenberg 1996; Hermisson and Wagner 2004; Rice 2004). Such a framework might provide a useful point of departure not only for separating the evolutionary importance of newly emergent versus newly expressed developmental variation but also for the connection between adaptation and adaptability. Considering that most adaptations in extant organisms undoubtedly result from developmental modifications and rearrangement of pre-existing components, greater integration of emergence and population genetic perspectives might have been mutually beneficial here. The author dismisses this opportunity however by admonishing the "self-styled evo-devos" (developmental evolutionary biologists) for "climbing on board" of the modern synthesis. But perhaps the reason for such climbing is that for all its deficiencies and often unrealistic assumptions, population genetics and its recent extension into developmental genetics, does provide a testable scientific framework, at least for the maintenance part of the evolutionary process, which emergence theory is perceived as lacking, even for the generative processes that are its primary focus. Thus, while emergent processes in physiology, biochemistry, and developmental biology are effectively invoked throughout the book with many examples, it is not clear how, for example, one would test that a particular novel form has started as an emergent process with no particular relationships with existing adaptations.

2 Evolution and Biological Emergences

The book introduces two types of evolutionary change: (i) progressive evolution—emergent processes involving internal and external inputs from embryological, symbiotic, physiological, and behavioral causes—resulting in a progressive increase in complexity, redundancy, and adaptability regardless of immediate differential fitness, and (ii) diversifying evolution—adaptive radiations in response to internal or external selection, in which selection hinders further innovations and preserves locally advantageous organism-environment associations. In this view, spurts of emergent evolution under novel or stressful conditions can be followed by diversifying selection, producing isolation of locally adapted forms, ultimately leading to speciation and a period of evolutionary stasis.

There are several defining features of emergent modifications: (i) they originate, amplify, and replicate regardless of immediate fitness consequences, often as a by-product of development, (ii) they can be produced by integration of multiple organismal units, by accumulation of prior adaptations, or through adaptability of regulatory mechanisms and associated changes in regulatory integration of complex structures, and (iii) they are often produced by combining different levels of organization, such as in symbiotic interactions, or in transitions to eukaryotic or multicellular organisms.

Whereas the second and the third of these features share some aspects with developmental population genetics and the theory of levels of selection, the first feature is unique in that it separates organismal variation into adaptive versus arising for reasons other than adaptation. This is an important distinction since the common view that all biological variation is either adaptive or soon-to-be adaptive shifts scientific inquiry from understanding the generative evolutionary processes to a search for an imbedded evolved plan—assigned variously to selection or genes—which popular media often portray as universal creators, architects, or sculptors of organismal forms. Another important contribution is the discussion of how emergent processes resulting from combining different levels of biological organization—from multicellularity to symbiosis to societies—can contribute to major evolutionary transitions (see also Margulis and Sagan 2002; Okasha 2006; Michod 2008).

But what are the drivers of emergence? What, for example, initiates, stops, and maintains internal selection for stress resistance (e.g., Whyte 1965)? The author makes a convincing point that abiotic and passive physical forces, rules, and constraints cannot account for discontinuity and increasing complexity of outcomes of emergent processes. But what does? It is true, as the author states, that "natural selection" can be replaced with "special creation" in some neo-Darwinian writings without the loss of logic, but could not the same thing be said about emergent processes? Perhaps the gaps in evolutionary theory cannot be solved by replacing external components of evolutionary progress with internal ones, or by elevating various components to the role of drivers of evolution, and instead we should explicitly focus on the nature of transitions that enable organism-environment systems to combine developmental induction of novelties, homeostasis, and evolutionary retention of already evolved forms.

3 Novel Synthesis or a More Realistic Perspective?

Even though criticism of the neo-Darwinian modern synthesis and particularly its selection-centered framework is a stated goal of the book, the modern synthesis and emergence theory address essentially different stages of an evolutionary continuum – correspondingly the maintenance and the generation of evolutionary change. Addressing the links between them could have illuminated a wider span of evolutionary process than did arguments about their causal primacy. The substantial perceived role of natural selection assigned by the modern synthesis, and rightly criticized in the book, might come not so much from its greater presumed evolutionary significance, but rather from a considerably narrower evolutionary

scope of the modern synthesis (the maintenance and modifications of existing adaptation over short evolutionary time) compared to other evolutionary theories, including emergence theory. Further, the history of evolutionary biology teaches us that focusing solely on either generation or maintenance processes is insufficient without explicit links to inheritance of these processes and their effects. The vagueness of these links in the book might preclude the reader from a greater appreciation of the evolutionary importance of the emergence theory.

Although continuity of inheritance from epigenetic retention to genetic assimilation is repeatedly invoked by the author to explain the maintenance of adaptation and major evolutionary transitions, the details of these processes in the context of emergence theory are not explained. For example, what accounts for transitions among inheritance systems in progressive and adaptive episodes of the emergence process and how do inheritance systems interact with each other? This is crucial if we are to understand how episodes of progressive evolution, that are said to progressively "liberate the organism from environmental influence" and give it "freedom of choice," do not close opportunities for subsequent environmental modifications and future "choices" needed for the adaptive evolution. Presumably such environmental liberation is maintained by increasingly genetic developmental control, but this would prevent not only adaptive environmental induction, but also further "natural experimentation" with emergence. Although the author implicitly invokes epigenetic inheritance for emergent processes and genetic inheritance for adaptations, this aspect is too important to be left unexamined.

The book contains many fascinating empirical examples and historical anecdotes. A non-specialist reader might find the extensive review of epigenetic and genetic processes and phenomena (from role of steroids to Hox genes) in the middle chapters helpful, while some biologists might find it somewhat disjoined and wish that referencing of original empirical research, especially for the most categorical and definitive statements, were more thorough and matched the extent of referencing in the first two chapters. The first two and the last two chapters are well edited and explicitly focused on the stated goal of the book, while the writing in some middle chapters is sometimes repetitive and less focused on the overall theme of the book, although the discussion of empirical examples here is interesting and stimulating.

The author's strong opinions about evolutionary processes are refreshing and thought provoking, his rigorous criticism of the neo-Darwinian theory of evolution reminds us of the necessity to explicitly recognize the theory's assumptions, and his excellent command of the literature is a sobering and timely reminder that many new theories are often well forgotten ideas of the past with a rich and fascinating history. Overall, the book succeeds in drawing attention to an under appreciated aspect of the evolutionary process and will undoubtedly contribute to a far more realistic evolutionary understanding of life's complexity and diversity.

References

Badyaev AV (2005) Stress-induced variation in evolution: from behavioral plasticity to genetic assimilation. Proc R Soc Lond Biol Sci 272:877–886

Chetverikov SS (1926) On certain aspects of the evolutionary process from the standpoint of modern genetics. J Exp Biol Series A 2:1–40
Cheverud JM (1996) Developmental integration and the evolution of pleiotropy. Am Zool 36:44–50
Eldredge N (1985) Unfinished synthesis: biological hierarchies and modern evolutionary thought. Oxford University Press, Oxford
Hermisson J, Wagner GP (2004) The population genetic theory of hidden variation and genetic robustness. Genetics 168:2271–2284
Lewontin RC (1983) Gene, organism and environment. In: Bendall DS (eds) Evolution: from molecules to men. Cambridge University Press, Cambridge, pp 273–285
Margulis L, Sagan D (2002) Acquiring genomes: a theory of the origins of species. Perseus Books Group
Michod RE (2008) Sex and multicellularity as evolutionary transitions in individuality. In: Sterelny K, Calcott B (eds) Major transitions in evolution revisited. Konrad Lorenz Institute, Altenberg
Müller GB, Newman S (eds) (2003) Origination of organismal form: beyond the gene in developmental and evolutionary biology. The MIT Press, Cambridge
Newman SA, Müller GB (2000) Epigenetic mechanisms of character origination. J Exp Zool 288:304–314
Okasha S (2006) Evolution and the levels of selection. Clarendon Press, Oxford
Oyama S (2000) The ontogeny of information: developmental systems and evolution. Duke University Press, Durham
Reid RGB (1985) Evolutionary theory: the unfinished synthesis. Crom Helm, Beckenham
Rice SH (2004) Evolutionary theory: mathematical and conceptual foundations. Sinauer Associates, Sunderland, MA, USA
Schmalhausen II (1938) Organism as a whole in individual development and history. Academy of Sciences, USSR, Leningrad
Schmalhausen II (1969) Problems of darwinism. Nauka, Leningrad
Wagner A (2005) Robustness and evolvability in living systems. Princeton University Press, Princeton, NJ
Wagner GP (2001) The character concept in evolutionary biology. Academic Press, San Diego
Wagner GP, Altenberg L (1996) Complex adaptation and the evolution of evolvability. Evolution 50:967–976
Whyte LL (1965) Internal factors in evolution. George Braziller, New York
Williams GC (1966) Adaptation and natural selection: a critique of some current evolutionary thought. Princeton University Press, Princeton