

18th Altenberg Workshop in Theoretical Biology 2008

Toward an Extended Evolutionary Synthesis

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organized by Massimo Pigliucci and Gerd B. Müller

Konrad Lorenz Institute
for Evolution and Cognition Research
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The topic

More than 60 years have passed since the conceptual integration of several strands of evolutionary theory into what has come to be called the Modern Synthesis. Despite major advances since, in all methodological and disciplinary domains of biology, the Modern Synthesis framework has remained surprisingly static and is still regarded as the standard theoretical paradigm of evolutionary biology. But for some time now there have been calls for an expansion of the Synthesis framework through the integration of more recent achievements in evolutionary theory.

The challenge for the present workshop is clear: How do we make sense, conceptually, of the astounding advances in biology since the 1940s, when the Modern Synthesis was taking shape? Not only have we witnessed the molecular revolution, from the discovery of the structure of DNA to the genomic era, we are also grappling with the increasing feeling – as reflected, for example, by the proliferation of “-omics” (proteomics, metabolomics, “interactomics,” and even “phenomics”) – that we just don't have the theoretical and analytical tools necessary to make sense of the bewildering diversity and complexity of living organisms. By contrast, in organismal biology, a number of new approaches have opened up new theoretical horizons, with new possibilities for integration and expansion in evolutionary theory, such as EvoDevo, Niche Construction, Epigenetic Inheritance, and many more.

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Abstracts

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Chance, history, and natural selection

A topic of considerable interest and controversy concerns the contingency of evolutionary outcomes. Stephen Gould famously (or infamously) argued that replays of the “tape” of life will lead to widely different outcomes. And since then there have been many attempts to confirm or refute his thesis on the basis of controlled laboratory experiments, “natural experiments,” and computer simulations. My concern is not so much to adjudicate the controversy, as to analyze it. I will focus on one of the two senses of “contingency” employed by Gould and others, namely, the unpredictability of evolutionary outcomes. And I will emphasize one particular source of unpredictability, namely random variation, or more specifically still, the historical order in which random mutations occur. The contingency of evolutionary outcomes has been thought to undermine the “importance” of natural selection. One of the general questions at issue in my paper will be the meaning of claims about the importance of this or that evolutionary agent, and in particular what is at stake in debates about the relative importance of selection vs. variation.

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Properties and scope of an Extended Synthesis

The Modern Synthesis has been hailed as “a historical event that appeared to fulfill a project at least as deep as the Enlightenment project (or even deeper still) of unifying the branches of knowledge” (Betty Smocovitis). What, in comparison, can an Extended Synthesis be like? After investigating the various things “unification by synthesis” can mean in a post-reductionistic framework, I will try to list a number of necessary ingredients, with particular attention to institutional and other “non-epistemic” factors. I will also address the issue of the autonomy of biology in light of some complications that arise because of the “physicalization” of some biological disciplines such as systems biology.

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High-dimensional fitness landscapes

During the last 75 years Sewall Wright's (1932) metaphor of "fitness landscapes", which are also known as "adaptive landscapes", "adaptive topographies", and "surfaces of selective value", has been a standard tool for visualizing biological evolution, adaptation, and speciation. Wright's metaphor is widely considered as one of his most important contributions to evolutionary biology. The notion of fitness landscapes has also proved extremely useful well outside of evolutionary biology (e.g., in computer science, engineering, biochemistry, and philosophy). I will describe recent advances in the theory of fitness landscapes that explicitly account for the fact that biologically realistic fitness landscapes have extremely high dimensionality. I will also discuss evolutionary implications of the theoretical results on the properties on high-dimensional landscapes.

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The epigenetic turn: the challenge of soft inheritance

Among the lines of developmental-evolutionary research that have been neglected during the hegemony of the Modern Synthesis, I will consider three that can be called “epigenetic”. The first focuses on canalization and plasticity, their evolutionary effects and their own evolution; the second, which has its roots in the structuralist tradition, stresses the centrality of the inherent properties of biological matter that generate patterns of development; the third calls attention to control mechanisms that lead to cell memory and cell heredity, both within and between organisms. All three lines of research are part of the “epigenetic turn”, which is challenging the Modern Synthesis of evolution. My paper emphasises the third approach, which calls for the incorporation of soft inheritance into heredity and evolution. I discuss different types of epigenetic inheritance, examine the prevalence, stability and inducibility of cellular epigenetic variants, propose an expansion of the epigenetic research program, and enumerate the ways in which epigenetic control mechanisms have affected micro- and macro-evolution. I suggest that just as at the beginning of the 20th century the rediscovery of Mendel's laws and the chromosomal mechanisms underlying them led to profound changes in all branches of biology

including evolution, so today, a hundred years later, another aspect of heredity – epigenetic inheritance and the epigenetic control mechanisms underlying it – is driving a major transformation in our understanding of evolutionary biology.

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Patterns and processes in macroevolution

The need to more fully incorporate scale and hierarchy into the evolutionary synthesis is richly seen in the fossil record. These factors sharply diminish the predictive power of conventional short-term observations, and demand novel approaches to the evolution of form, the inclusion of ecology in macroevolutionary developmental biology, the role of sorting processes at levels above and below the organismic levels, and to a more complete theory of extinction and evolutionary rebound. Obvious indicators include (1) The nonrandom origins of evolutionary novelties in time and space; (2) the recent corroboration of evolutionary stasis as a pervasive species-level dynamic, and strong support for species selection in the broad sense (myriad examples) and in the strict sense (fewer well-documented cases, but potentially abundant); (3) the failure of positive and negative biotic interactions to translate simply into clade dynamics. Hierarchical approaches are essential to understanding long-term evolutionary processes.

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Facilitated variation

In evolution selection has been regarded as the creative force that shapes phenotypic variation into the refined adaptations of diverse organisms. Though phenotypic variation provides the raw material for selection, it has long been ignored because it seems random in direction, small in the increment of change, and non-limiting in amount, and because it is an effect of genetic variation, which is better understood. We argue that a molecular knowledge of the phenotype, particularly of its development and physiology, is needed to assess the number and targets of genetic changes effecting selected phenotypic change, that is, for a knowledge of how organisms really evolved. We integrate proposals about the generation of phenotypic variation into a theory of facilitated variation.

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The structure of evolutionary theory and biological knowledge: Epistemic materials for a 21st century synthesis

Much of the discussion about the adequacy of contemporary evolutionary theory has focused on its content, such as whether it integrates developmental considerations. A different approach is to explore the form or structure of evolutionary theory, which is in part a philosophical question about the nature of scientific theories. In this paper I adopt the latter route in order to introduce some epistemic materials for a 21st century synthesis. Specifically, I distinguish narrow and broad interpretations of

evolutionary theory and argue that a broad interpretation is more appropriate for conceptualizing an expanded evolutionary synthesis (e.g. one that includes development). This requires construing the structure of evolutionary theory as multiple problem domains exhibiting complex but coordinating relationships. As a consequence, we can observe a new perspective on the structure of biological knowledge and gain a concrete understanding of how ‘nothing makes sense except in the light of evolution’.

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Epigenetic innovation theory

The Modern Synthesis, based on a population genetic variation paradigm, addresses phenotypic evolution from the perspective of variation and adaptation of characters but sidesteps the problem of how these characters arise. Epigenetic innovation theory argues that primordial forms and phenotypic novelties represent a specific class of phenotypic change that differs from adaptive variation. It also introduces a distinction in the causal mechanisms underlying variation and innovation. Whereas adaptive variation resides in the classical interplay between genetic variation and natural selection, the causality for phenotypic innovation is seen to lie in the epigenetic properties of developmental systems, such as cell and tissue self-organization, generic material effects, and non-linear interaction dynamics. Vertebrate limb development will be used as an example system. The inclusion of innovation theory into an Extended Synthesis framework expands the explanatory reach of evolutionary theory to non-gradual and non-adaptive phenomena of phenotypic evolution and provides a modified understanding of the causal roles of natural selection.

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Dynamical Patterning Modules: A “pattern language” for development and evolution of metazoan form

We consider the role played by a core set of dynamical patterning modules (DPMs) in the origination, development and evolution of the Metazoa. These consist of the gene products of what has come to be known as the metazoan “developmental-genetic toolkit,” but considered in subsets, as dynamical networks embodying physical processes characteristic of chemically and mechanically excitable mesoscopic systems like cell aggregates: cohesion, viscoelasticity, diffusion, and spatiotemporal heterogeneity based on lateral inhibition, and multistable and oscillatory dynamics. The DPMs are distinguished from developmental transcription factors (DTFs), products of a separate set of toolkit genes which function as multistable networks to control cell-type identity. We show how DPM-associated gene products and pathways that preexisted the metazoa acquired novel morphogenetic functions simply by virtue of the change in scale and context inherent to multicellularity. The concept that DPMs constitute a “pattern language” for metazoan form implies that the multicellular organisms of the late Precambrian-early Cambrian were phenotypically highly plastic, fluently exploring morphospace in a fashion decoupled from both function-based selection and genotypic change. The relatively stable developmental trajectories and morphological phenotypes of modern animals are proposed to be products of stabilizing selection.

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Niche construction and niche inheritance

Niche construction theory introduces ecological inheritance to evolution (Odling-Smee et al. 2003). Ecological inheritance is the inheritance of natural selection pressures previously modified by ancestral niche-constructing organisms. Descendant organisms inherit genes and biotically transformed selection pressures in their external environments. The combined inheritance is called niche inheritance. Niche inheritance is used as a basis for classifying several genetic and non-genetic inheritance systems currently being proposed as possibly significant in evolution (e.g., Jablonka and Lamb 2005). Niche inheritance has novel implications for both the “evo-devo” relationship; development becomes a process of active niche regulation by plastic niche-constructing phenotypes; and the “devo-evo” relationship; it proposes new ways in which the prior development of individuals could influence the subsequent evolution of populations. Both are discussed.

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Phenotypic plasticity as causal factor in evolution

The concept of phenotypic plasticity has undergone a remarkable trajectory since its inception at the beginning of the 20th century. Introduced at the same time of the realization of the difference between genotype and phenotype, it has been in the background of evolutionary theory and empirical research for many decades. It underwent a renaissance beginning in the mid-1980s, and papers on plasticity now regularly appear in evolutionary journals. Still, there is much confusion among biologists about what plasticity is, and more importantly about the role it plays in our understanding of organic evolution. In this talk I will explore the place of phenotypic plasticity in an Extended Evolutionary Synthesis, with a particular focus on how it inter-plays with research in evo-devo and on epigenetic inheritance, as well as on the sort of light plasticity may shed on standard evolutionary concepts such as pre-adaptation and mosaic evolution.

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Epistasis, selection, and the evolutionary synthesis in the age of genomics

Genome science has provided us with an unprecedented glimpse into the structure of the genetic component of organisms and how these are expressed in complex interacting networks. The impact of genomics on the study of the evolutionary process has been revolutionary, and has impinged on all aspects of evolutionary thought. We will discuss two issues of central importance to evolutionary biology, the nature of selection on the genome and epistasis in the context of genomic networks, in which data and approaches from genome science provide the basis extending our understanding of evolutionary genetics as set forth in the Modern Synthesis.

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Evolution by natural selection in the brain

A new synthesis of evolution includes extending the evolutionary paradigm to domains that are not at the level of genes or organisms. I shall discuss two such important cases. The first is the field where chemical and biological evolution overlap, and it is of paramount interest for the origin of life. I shall discuss what we do know and what we suspect in this domain from the point of view of evolutionary theory. In the second part I look at 'selectionist' approaches to brain dynamics. I shall propose a mechanism for copying of neuronal networks that is of considerable interest for neuroscience for it suggests a neuronal basis for causal inference, function copying, and natural selection within the human brain. To date, no model of neural topology copying exists. As a proof of principle, our mechanism of topographic map formation coupled with Spike-Time Dependent Plasticity (STDP) can copy neuronal topology motifs. We also demonstrate an ancillary topological error correction mechanism that can improve neuronal copying fidelity. In both cases I shall reflect on problems of evolvability.

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Modularity, evolvability, and the evolution of genetic architecture

One way evolutionary theory has changed over the last decades is a renewed interest in the evolutionary forces that shape systemic properties of organisms. That is to say that classical population genetic theory focused on the dynamics of one or a few genes under mutation, selection and recombination and drift, or on aspects of evolutionary dynamics that can be understood by “mean field” approximations of large number of genes, i.e. quantitative genetics. These approaches have foundational value in explaining how evolution proceeds but the theoretical tools do not easily translate into an understanding of the evolution of variational properties and genetic architecture. In the last ten years a lot of progress was made in understanding the principles that may lead to the evolution of genetic and environmental robustness, which depends largely on indirect selection forces. More recently increasing evidence from simulation studies suggests that evolvability is also an evolvable property, but it turns out that these results are even harder to fit into the mold of the classical model of selection as fitness optimization. I will discuss two recent studies which show that 1) evolvability is increasing under very general conditions, and 2) that this fact is probably due to a complex interaction between invasion probabilities and resistance to invasion that push the system towards genotypes with higher evolvability. Hence it seems that a newer evolutionary synthesis will have to include explanatory models that go beyond selection for a focal trait or drift determined by mutation pressures.

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Multilevel selection, major transitions, and human evolution

I will attempt to make three contributions toward an extended evolutionary synthesis. First, I will describe what I regard as the final resolution of the multilevel selection controversy, which need not be obscured by current discussions about pluralism. Second, I will relate multilevel selection theory to the concept of major transitions, which has become so justly influential during the last few decades. Third, I will show that human evolution qualifies as a major transition, even more than imagined by Maynard Smith and Eörs Szathmary in the 1990's. In general, the 21st century will witness an integration of knowledge about humanity comparable to the integration of the biological sciences during the 20th century. Future historians will see this as the most important feature of the extended evolutionary synthesis.

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Gene regulatory networks and natural selection

Evolutionary biologists have often treated genes in isolation -- isolated from other genes, independent of function, and detached from phenotype and the environment. To a large extent, this has been a sociological phenomenon, not a deficiency of theory. During the 1990s, evolutionary developmental biologists re-focused attention on genes as components within networks; they also emphasized understanding changes in molecular and cellular function, and how these changes influence organismal phenotype. Our group has investigated these phenomena in a variety of organisms. We have focused on gene expression as a particularly informative aspect of phenotype because transcription requires gene interactions, is exquisitely sensitive to environmental influences, is susceptible to detailed functional analyses in a comparative framework, and phenotypic and fitness consequences can be assessed. These studies illustrate how treating genes in isolation results in an incomplete view of evolutionary processes and reveal hitherto unsuspected evolutionary phenomena.
