16th Altenberg Workshop in Theoretical Biology 2007

# The Major Transitions Revisited

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organized by Brett Calcott and Kim Sterelny

Konrad Lorenz Institute
for Evolution and Cognition Research
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## *The topic*

It is now ten years since John Maynard-Smith and Eors Szathmary published their The Major Transitions in Evolution. That monograph developed an overall framework for understanding the evolution of life. Maynard-Smith and Szathmary understood the evolution of complexity as the coupling of two processes: an expansion of the mechanisms of heredity, as richer and more accurate systems of the intergenerational flow of information evolved, and as the evolution of new levels of biological individuality, as previously independent lineages in Darwinian populations came to share their evolutionary fate. The time is ripe for a workshop assessing and developing their framework, and comparing it to others. For there are now available much better confirmed phylogenies of the major branches of the tree of life; the fossil record, likewise, is much better known and understood, and there have been important developments in evolutionary theory; in particular, on integrated evolutionary and developmental biology and in the development of multi-level theories of selection. Both these are of special importance to the major transitions; especially those involving transitions to multicellularity.

## ***Program***

Brett Calcott & Kim Sterelny Is The Metazoan Radiation a Major Transition?
Samir Okasha Evolutionary Transitions, Levels of Selection, and Cross-Level Byproducts
Kim Sterelny Evolvability Reconsidered

Rick Michod Evolution of Individuality During the Transition From Unicellular to Multicellular Llife
Peter Godfrey-Smith Darwinian Populations and Transitions in Individuality
Ben Kerr Setting the Stage for a Major Transition: The Evolution of Restraint in Structured Populations

Brett Calcott Internal Signalling and the Division of Labour
Michael Lachmann Evolution and Information
Carl Simpson Empirical Insights into Multilevel Selection through Transitions from Solitary to Colonial Organisms

Andrew Knoll The Early Evolution of Multicellular Organisms: Phylogenetic, Geologic, and Functional Perspectives
Alirio Rosales What's an Evolutionary Transition? Causal Dependence, Adaptation, and Evolvability
Lindell Bromham DNA and Deep Time: What, if anything, can Molecular Data Tell us about the Cambrian Explosion?
Eörs Szathmáry *In silico* Evolutionary Developmental Neurobiology and the Origin of Natural Language

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## *Abstracts*

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### DNA and Deep Time: What, if Anything, can Molecular Data tell us about the Cambrian Explosion?

In “The Major Transitions in Evolution”, John Maynard Smith and Eors Szathmary said “The Cambrian explosion remains a puzzle…the puzzle is why the Cambrian explosion took place when it did”. The timing of the diversification of the animals may hold the key to understanding why it happened. The fossil record shows a dramatic transition from simple soft-bodied creatures to complex animals with hard parts during the latest Precambrian and early Cambrian. But can we trust the fossil record? The amount of genetic divergence between these lineages is far more than we would expect from only half a billion years of evolution, so dates of divergence based on molecular data place the diversification of animals deep in the Precambrian. But can we trust the molecular dates? I will give a rough guide to molecular dating, and discuss the way that molecular data can be used to test hypotheses about unique events that occurred in evolutionary deep time.

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### Internal Signaling and the Division of Labour

In the "Major Transitions", Maynard Smith and Szathmáry identify a number of general processes that have occurred repeatedly over evolutionary time and at different levels of biological organization. Here, I follow one interesting theme they remark upon. An analogy is drawn between the division of labour in society and differentiation in multicellular organisms: both depend on a second inheritance system (language and methylation, respectively). I argue that inheritance is not a useful way to think about this analogy. Instead, I recast the analogy in terms of internal coordination and evolution of signaling. I explore some ways to think of this process in very general terms, look at some connections with evolvability, and link it back to the problem of enabling new levels of organization.

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### Darwinian Populations and Transitions in Individuality

Many major transitions in evolution involve the appearence of new higher-level 'individuals,' emerging from cooperating collectives of lower-level entities. Examples include the evolution of the eukaryotic cell, and the evolution of multicellularity. It is often unclear when, in this process, a new higher-level individual should be recognized as real. Some discussions of the case of multicellularity emphasize reproductive specialization, for example; others regard this criterion as too restrictive. I approach these topics via a general treatment of 'Darwinian populations,' combining traditional summaries of the evolutionary process with input from recent work in the philosophy of science. (This talk will overlap with, but not be identical to, my talk at ISH. The same basic framework will be introduced but the details and case studies will be different.)

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### Setting the Stage for a Major Transition: The Evolution of Restraint in Structured Populations

One of the characteristics of a major transition is that entities that were previously autonomous come to depend on a greater whole for reproduction and survival. However, unrestrained use of common resources by a subset of entities in the collection constitutes an Achilles heel of the major transitions. For instance, meiotic drive, cancer development, and social cheating involve unrestrained use of common resources in diploid reproduction, multicellular organisms, and societies. One step towards a functional higher level involves the emergence and maintenance of competitive restraint. Here I will argue that competitive restraint can evolve very naturally under two conditions: (i) the populations of entities are spatially structured and (ii) the ecological interactions between entities are intransitive (e.g., A beats B, B beats C, and C beats A). I will illustrate these ideas with two microbial systems. The first system involves toxin-producing bacteria, toxin-sensitive bacteria and toxin-resistant bacteria satisfying a rock-paper-scissors relationship. In a spatially structured habitat, an evolving bacterial strain will not maximize its competitive ability in this community. The second system involves a host-pathogen relationship between bacteria and viruses, which plays out in a metapopulation context. With spatially restricted migration, the evolving viral pathogen evolves
significant restraint. In both these systems, an intransitive ecological dynamic sets up a type of negative feedback and population structure ensures that this feedback is experienced disproportionately by the unrestrained type. I will discuss the likelihood that this process operates in other systems and how such restraint might set the stage for major transitions.

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### The Early Evolution of Multicellular Organisms: Phylogenetic, Geologic, and Functional Perspectives

Simple multicellular organisms form a heterogeneous grouping that defies simple phylogenetic, functional or developmental categorization. Most, however, share the functionally important property that every cell is in direct contact with the external environment, at least during phases of the life cycle characterized by nutrient acquisition. In contrast, the complex multicellular organisms found within the animals, streptophytes, fungi, red algae, and brown algae, have a multicellular organization in which only some cells interface directly with the environment. In consequence, cells do not have equal access to nutrients and will not accumulate biomass at a uniform rate - unless a mechanism evolves for the transfer of resources from one cell to another. Indeed, only active transfer processes will free such organisms from the strong constraints of molecular diffusion. Interior cells cannot receive signals directly from the environment, although response to environmental dynamics remains key to growth, reproduction, and survival. Complex multicellular organisms, therefore, require mechanisms by which environmental signals can be received by surficial cells and transduced to interior cells, where genes will be up- or down regulated in response.
The fossil record indicates that simple multicellularity evolved early (> 1200 Ma) in the Eucarya, but complex and macroscopic animals and algae radiated only near the end of the Proterozoic Eon, more or less coincident with the advent of persistently oxic deep waters in the oceans. Only the oxidation of organic molecules by 02 provides sufficient energy to build a food chain that includes macroscopic heterotrophs, and only oxygen in concentrations approaching those ofthe present day permits the

oxygenation of interior cells in macroscopic organisms limited by diffusion. The long apparent lag between the appearance of simple multicellularity in eukaryotes and the radiation of groups with complex multicellular organization, thus, has an environmental component that can be linked back to the consequences of life with interior and exterior cells.

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### Evolution and Information

What is a signal worth, how much information does it carry? The notions of entropy and mutual information have not made it into mainstream biology. Instead, the value of signals is measured in more tangible currency, such as number of offspring or fitness. In this talk I will show that the notion of biological fitness, or growth rate, and measures of information are tightly linked. I will then explore the information content of the genome. How does information enter the genome, and what benefit can it give once it is there.

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### Evolution of Individuality During the Transition From Unicellular to Multicellular Life

How and why do groups become individuals? These are the central questions motivating our work. We consider the problem of the origin of multicellularity and the transition from groups of undifferentiated cells to groups of differentiated cells specialized at reproductive and vegetative (viability enhancing) functions. Our theory predicts that the trade-off between fitness components (viability and reproduction) is a major factor driving this transition. In particular, we predict that the convex curvature of the trade-off selects for specialization and that the curvature shifts from concave to convex as cell-group size increases. We have tested our models in two ways by taking a how and why approach. We have studied the origin of the genetic basis for reproductive altruism in the multicellular Volvox carteri by showing how an altruistic gene may have originated through co-option of a life-history trade-off gene present in a unicellular ancestor. Second, we ask why reproductive altruism and individuality arise only in the larger members of the volvocine group (recognizing that high levels of kinship are present in all volvocine algae groups). Our answer is that the selective pressures leading to reproductive altruism stem from the increasing cost of reproduction with increasing group size which creates a convex curvature of the trade-off function.

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### Evolutionary Transitions, Levels of Selection, and Cross-Level Byproducts

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This paper examines a philosophical issue arising from the biological literature on evolutionary transitions. According to a widely held view, multi-level selection is crucial for understanding evolutionary transitions, for such transitions involve a number of free-living individuals, originally capable of surviving and reproducing alone, coming together to form a group; therefore, there is the potential for selection to operate at both the individual and the group level during a transition. In any such multi-level scenario, it is important to consider the potential interaction between the two levels of selection. Additionally, it is important to ask whether one level of selection might ‘causally exclude’ another, i.e. whether selection at one level might generate, as an unintended side-effect, a character-fitness covariance at another level, higher or lower, and thus the appearance of direct selection at that level. I argue that such ‘cross-level byproducts’ are likely to be ubiquitous during the early stages of evolutionary transitions, when the ‘groups’ are still loose coalitions of interacting individuals. This is illustrated with reference to Michod’s models for the evolution of multi-cellularity. Finally, I show that the notion of a cross-level byproduct suggests a natural answer to the question of when a group of lower-level individuals constitutes a genuine evolutionary unit.

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## What’s an Evolutionary Transition? Causal Dependence, Adaptation, and Evolvability

Ever since Darwin, a major tenet of evolutionary thinking is that the mechanism of natural selection acting in the present has acted in the past in comparable ways. This involves an extrapolation of present natural selection to natural selection as a historical mechanism. Such understanding comes from how our modelling efforts and how the latter eventually match studies in experimental or field systems in illuminating ways. I wish to distinguish two senses of historicity for natural selection. Locally, natural selection preserves certain configurations given that they have certain degree of approximate stability. Globally, such configurations have originated in the evolutionary process itself. Whatever adaptive complexity we can now discern using our models and experiments, it ought to have been originated in the course of evolutionary history: any present configuration must have been structured from previous existing configurations. A central problem for our understanding of evolution by means of natural selection is to explain life’s historicity in the global sense as an evolutionary movement in a space of possibilities of complexity. I will understand an ‘evolutionary transition’ as a movement in such a space and will understand historicity in the global sense as a thesis of the causal dependence of a given configuration on the previous one: in any ‘major transition’, a ‘new level’- e.g., multicellularity - is causally dependent on a previous one – e.g., unicelularity. How are we to understand such causal dependence? What can we learn from models of evolutionary transitions on this regard? These are questions that I wish to explore here.

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## Empirical Insights into Multilevel Selection through Transitions from Solitary to Colonial Organisms

Major transitions in evolution occur when a new hierarchical level of organization is incorporated into organisms. When this occurs, the dominant level of selection shifts to the highest level of organization in two phases. The first is the emergence of a new level through the aggregation of organisms, followed by the individuation of that new level. The two classes of models of multilevel selection roughly correspond to these phases. The set of multilevel selection models are heterogeneous enough that distilling the biologically important insight is difficult. However, a number of workers have suggested that propagule size is critical for the efficacy of the higher level of selection over the lower level of selection. They note that a small propagule size works because it maximizes the heritability of group-level adaptations. Also note that small propagule size also effectively shifts the time-scale of selection from that of the constituents to that of the group because group reproduction is then contingent on the successful survival of that propagule. I suggest that the propagule size parameter is best measured as the proportion of the group that does not reproduce, the non-reproductive ratio (NRR). Colonial organisms provide almost continuous variation across the full range of possible NRRs, many primitive groups with a NRR of zero and many with NRRs approaching one. Preliminary data show that colonial organisms with low NRR are weakly individuated and that a positive correlation between NRR and individuation is present across 189 taxonomic groups within 13 phyla and 3 kingdoms.

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## Evolvability Reconsidered

Some lineages are much more diverse and much more apparently disparate than others; thus the Metazoans have evolved in the last 500 million years a spectacular array of morphologies and a formidable number of species. In contrast, some other multicelled lineages (for example volvox and its relatives) exhibit limited diversity and disparity. It is plausible to suppose that such differences are in part explained by differences in evolutionary plasticity or flexibility: lineages differ in evolvability. In the last ten years, evolvability has become a hot topic in evolutionary biology. In this literature, four different strands have emerged. Some of the evolvability literature has focused on properties of replication systems: what features of the cross-generation transmission of developmental resources make lineages more plastic; which make them less plastic. This was the slant on evolvability in Major Transitions, and also in my own earlier work. But there is another strand of the literature that focuses on developmental systems; on differences in the use of these resources. This line of thought is particularly evident in the discussion of modularity and entrenchment in evo-devo. Thus it is argued that traits in a lineage are evolutionarily plastic only if they develop (fairly) autonomously. This contrast between development-focused and replicator-focused models of evolvability cross-cuts a quite different contrast: between models of evolvability that explore population-level properties and their consequences (as in Eldredge's model of evolutionary stasis) and those that explore the properties of individual organisms. My aim in this paper is to probe the relationships between these approaches to evolvability in the context of the Cambrian radiation.

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## *In silico* Evolutionary Developmental Neurobiology and the Origin of Natural Language

It is justified to assume that part of our genetic endowment contributes to our language skills, yet it is impossible to tell at this moment exactly how genes affect the language faculty. In this work we aim to complement experimental biological studies by an in silico approach in that we simulate the evolution of neuronal networks under selection for language-related skills. At the heart of this project is the Evolutionary Neurogenetic Algorithm (ENGA) that is deliberately biomimetic. The design of the system was inspired by important biological phenomena such as brain ontogenesis, neuron morphologies, and indirect genetic encoding. Neuronal networks were selected and were allowed to reproduce as a function of their performance in the given task. The selected neuronal networks in all scenarios were able to solve the communication problem they had to face. The most striking feature of the model is that it works with highly indirect genetic encoding just as brains do.