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Session: Hierarchy Theory of Evolution, Wednesday, July 13th

The session – proposed by Telmo Pievani and Emanuele Serrelli, University of Milano Bicocca – discusses Hierarchy Theory with eminent paleontologist Niles Eldredge and 10 other scholars. Hierarchy Theory assumes that the evolutionary disciplines have an ontological basis for their existence, i.e. systems with peculiar spatiotemporal dimensions, origins, histories, demises, and internal dynamics leading to stability and change through time. The theory is developing around Eldredge's recognition of at least two main distinct evolutionary hierarchies - the genealogical and the ecological - and around a general vision of evolution as a process of interactions at various scales. E.g., macro-evolutionary patterns are explained by a "sloshing bucket" model, where ecological events reverberate in the evolutionary hierarchy.

MORNING SESSION 1:
- BROOKS, Dan - Metaphors for the Extended Synthesis: Something Old, Something New.
- CAIANIELLO, Silvia - Modularity and Hierarchy Theory.
- CAPORAEL, Linnda - Grounding Human Social Cognition in Hierarchical Group Structure.

MORNING SESSION 2:
- DIETL, Gregory - Toward a Unified Ecology in Macroevolution.
- ELDREDGE, Niles - A Matter of Individuality: Hierarchy Theory at the Dawn of Evolutionary Biology.
- MILLER, William - Macroevolutionary Consonance and expansion of the Modern Synthesis.

AFTERNOON SESSION:
- PIEVANI, Telmo - The Evolving Structure of Evolutionary Theory: the role of Hierarchy Theory for an Extended Evolutionary Synthesis.
- TËMKIN, Ilya - Nested Networks and Biological Diversification.
- BRYSSE, Keynyn – Lessons from Interdisciplinary (Non-) Communication in the Mass Extinction Debate.
- SERRELLI, Emanuele - Criticizing Adaptive Landscapes and the Conflation Between Ecology and Genealogy.

Keywords: Ecology Systematics Population Genetics Evolutionary Theory Development Organismal Paleontology Macroevolution

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Dan R. BROOKS[1]

Metaphors for the Extended Synthesis: Something Old, Something New

Abstract: Darwin's original formulation of evolutionary theory was complex and elegant, rich in metaphors based on natural history observations. It was immediately criticized for being too complex and metaphor- riddled. Biologists responded by simplifying the theory and removing most naturalistic metaphors. The result was Neo-Darwinism or The New Synthesis, which dominated evolutionary biology in the 20th century. In the 1980s, coincident with the 100th anniversary of Darwin's death, a broad coalition of biologists characterized Neo-Darwinism as inadequate to accommodate information being generated by molecular biology, developmental biology and systematics. The people making the critiques were rejected out of hand, but the status quo community set to work co-opting their interesting ideas. Recently, coincident with the 200th anniversary of Darwin's birth and the 150th anniversary of the publication of Origin of Species, an "Extended Synthesis" has been announced. This emerging technical framework restores the wonderful complexity of Darwin's original proposal, and extends it in ways that might have amazed even Darwin. I propose some of the metaphors necessary to explain the new theory to the world at large.

Keynyn BRYSSE[2]

Lessons from Interdisciplinary (Non-) Communication in the Mass Extinction Debate

Abstract: On June 6, 1980, an article entitled "Extraterrestrial cause for the Cretaceous-Tertiary extinction: experimental results and theoretical interpretation" appeared in Science. Its authors – physicist Luis Alvarez, his son, geologist Walter Alvarez, and nuclear chemists Frank Asaro and Helen Michel – presented evidence that an asteroid or comet had hit the Earth 65 million years ago, and argued that it caused the mass extinction known to have occurred at that time. Scientists of many fields embraced the Alvarez impact hypothesis and began searching for further physical evidence of the impact. Some scientists argued that the physical evidence suggested a volcanic eruption instead of an impact, whereas others (primarily

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vertebrate paleontologists) argued that the biological evidence points to neither volcanism nor an impact as the (sole) cause of the K-T mass extinction. Vertebrate paleontologists had several sound scientific reasons for skepticism, including fossil evidence documenting a pattern of victims and survivors more complex than could be explained by either impact or volcanism. Paleontologists also resented the intrusion into their domain by disciplinary outsiders who did not appreciate the complexity of the fossil record and the pattern of the history of life. I have identified several sources of communication problems in this debate between experimental scientists (including the Alvarez team) and historical scientists (such as paleontologists). In my talk I will explore these problems and their implications, including different ways of framing research questions, and differing ideas regarding what counts as relevant evidence in answering questions about the K-T extinction. The debate over the cause(s) of the K-T and other mass extinctions forms a rich case study of interdisciplinary scientific debate, in which not only the answers, but the standards of evidence, and even the questions that can and should be asked, are shifting and contested territories.

Silvia CAIANIELLO[3]

Modularity and Hierarchy Theory

Abstract: In Herbert Simon's influential paper on the architecture of complex systems in 1962, hierarchy and nearly-decomposability (later relabelled as modularity) were inextricably entrenched notions. The higher "evolvability" and stability of hierarchical systems was namely due to their characteristic organization in sub-assemblies – "self-organising chinese boxes" – whose very nesting gave origin to different and relatively autonomous levels in force of their "loose" vertical coupling. While endorsing Simon's argument for the autonomy of levels, however, the hierarchical theory of biological evolution in the 1980s did not find an equally systematic place for the "loose" horizontal coupling, or the modular organisation of hierarchical systems. Only in the late 1990s, after modularity became a pivotal notion in Evo-Devo, Robert Brandon incorporated at least the veritable "evo-devo" modules as relevant "units of selection" at the organismic level, for addressing the issue of the "quasi-independence" of characters in adaptive evolution, raised by Richard Lewontin in 1978. I will focus on two issues: 1. how far a modular understanding of organisms might modify the notion of units of selection and the representation of interlevel dynamics; 2. whether such an understanding could contribute to the merging of the two hierarchic traditions (integrationist and scalar) highlighted by Stanley Salthe.

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Linnda CAPORAEL[4]

Grounding Human Social Cognition in Hierarchical Group Structure

Abstract: Neo-Darwinism generated considerable excitement in some areas of psychology. The interest was less about Darwinism's potential revolutionary implications--although these were widely anticipated--than the belief that "selfish genes" would at last ground psychological science, thereby giving it the legitimacy to ground other disciplines in the human sciences. The hope for a Darwinian revolution in psychology was necessarily weak. A theoretical perspective—individual "genetic" self-interest—that explained the transmission of biological traits in humans (and all other life forms) was arguably irrelevant to answering the main questions about which traits were "biological," as opposed to learned or cultural. However, three significant advances, accumulating over the last decade, have eased the way for a broad-based human evolutionary studies. One is evo-devo, which brings development and ecology, into the evolutionary conversation, by focusing on bodily form and its transformation through time. Another is an unprecedented interest in the role of embodiment (which has a number of meanings) for understanding human activity and mind. The third is an undertheorized acknowledgement that "humans are social." I propose a hierarchical model of face-to-face group structure and dynamics. The dynamical structure originates in the joint consideration of group size and tasks. Components of this hierarchical structure occur in everyday life, in the course of development, and plausibly, are repeatedly assembled over the course of human evolution. Although simple, the model has considerable force for constraining and revitalizing evolutionary and cultural perspectives on human development, culture and cognition.

Gregory P. DIETL[5]

Toward a Unified Ecology in Macroevolution

Abstract: The role that ecology plays in macroevolution is controversial. Historically, this role has been evaluated from two philosophical viewpoints: 1) simple extrapolation of ecological processes that occur at the level of individual organisms, and 2) interaction of genealogical and ecological systems that are arranged hierarchically, with smaller units forming the components of larger systems. I will use a heuristic metaphor of change—panarchy—introduced by

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Holling (2001) to better understand transformational change in ecological systems as a conceptual bridge between these two approaches. The term panarchy has been introduced to capture the evolutionary nature of a nested set of "adaptive cycles" of ecological systems across space and time scales. Panarchy illustrates how fast and slow and small and big events and processes can transform ecological systems through evolution. It also presents, in contrast to orthodox views, a hierarchical framework that explicitly separates conventional levels from scale-dependent levels in space and time. I will explore how best to integrate this theory to suggest specific testable hypotheses to explain long-term patterns in the history of life.

Niles ELDREDGE[6]

A Matter of Individuality: Hierarchy Theory at the Dawn of Evolutionary Biology

Abstract: A hierarchical perspective was present at the dawn of evolutionary theory. The Italian geologist Giambattista Brocchi (1814) suggested (1) that species have births and deaths analogous to those of individual organisms; and (2) that species have intrinsic longevities. Brocchi had concluded from his work on Tertiary marine invertebrates that extinction is primarily a reflection of species growing old and dying, rather than the result of environmental events. Brocchi's work was reviewed by Horner (1816) in Edinburgh—a hotbed of radical, pro-transmutational thinking—and Brocchi was well-known and respected in the British scientific community. His analogy appears (though without attribution) in the increasingly-notorious Anonymous essay of 1826 in the first volume of Jameson's Edinburgh New Philosophical Journal and in other prominent publications in the 1820s. Darwin's early work on Argentinian fossils at Bahia Blanca began his close examination of spatiotemporal replacement patterns of species three years before he reached the Galapagos. Both components of Brocchi's analogy are present in Darwin's essay February 1835—and is explicit in his Red Notebook passages of early 1837. Indeed, Darwin letter to Jenyns in 1844, saying that his initial exploration of the "question of the immutability of species, i.e. whether species are directly created, or by intermediate laws, (as with the life and death of individuals)"—constitutes a clear statement on the importance of Brocchi's analogy in Darwin's earliest transmutational work. Darwin's initial transmutational theory—essentially a geographically-based, saltational model of species origins—was developed directly from seeing species as individuals, and applying the two components of Brocchi's analogy to his own in-the-field empirical data on spatiotemporal species replacement patterns in southern South America. Thus hierarchy theory was foundational to the origin of evolutionary theory as we know it today. (with Stefano Dominici)

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William MILLER, III[7]

Macroevolutionary Consonance and expansion of the Modern Synthesis

(See Miller's submission). A true expansion of the synthesis is growing out of paleontology in the form of attempts by various workers to link long-term development of large ecologic systems (paced by climate changes and geologic processes) to speciation processes and patterns. Examples include Elizabeth Vrba's turnover pulse hypothesis, Niles Eldredge's sloshing bucket model, and what I have referred to as macroevolutionary consonance. Coordinated stasis is a related concept that emphasizes pattern over process. Since at least the early 1800s we have known that the fossil record is characterized by 'punctuations' at varied scales, often involving 'regional regimes' of plant and animal species that appear together and disappear together in the rock record—the very thing that makes biostratigraphy work. The new idea is that macroevolutionary and regional ecologic processes are not simply synchronized or take place at the same spatiotemporal scale, but that they are probably causally coordinated. This kind of coordination is related to regional disturbances and reorganizations/replacements of large ecologic systems. Most of the adaptive speciation in the Phanerozoic (the last 542 My when the fossil record has been rich enough to resolve such patterns) may have resulted from crashes and recoveries of regional ecosystems, producing waves of new species in new ecologic configurations, persisting for 105 – 107 yr with only minor subsequent embellishments or alterations until the next turnover event. If this turns out to be a genuine expansion of the synthesis we will have to return to E. Hutchinson his famous book title, The Ecological Theater and the Evolutionary Play (usually reconfigured as 'evolution takes place on an ecological stage') and think of a new trivialization of the relation of evolution and ecology that represents more accurately the close connections between the origin of (the most important?) species and development large-scale ecologic systems.

Telmo PIEVANI[8]

The Evolving Structure of Evolutionary Theory: the role of Hierarchy Theory for an Extended Evolutionary Synthesis

Abstract: Evolutionary theory shows a 150 years history of theoretical and empirical extensions and revisions, without any apparent radical change of "paradigm" and without a rival Research Programme able to replace it. The ongoing

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possible transition from the Modern Synthesis to a so-called "Extended Evolutionary Synthesis" (EES) is here interpreted through the Methodology of Scientific Research Programmes, proposed by the epistemologist Imre Lakatos and updated. A wide and detailed consideration of the interactions between the Genealogical Hierarchy and the Ecological Hierarchy of evolution, at different nested levels, seems the most relevant theoretical innovation able to give coherence to a highly heterogeneous set of new evidences and data. In a Neo-Lakatosian approach, the current situation in evolutionary biology could be represented by a "progressive" shift of the standard research programme, moving from the quite rigid theoretical framework of the population genetics version of Modern Synthesis (gradualism, gene-centrism, adaptationism) to the more inclusive and pluralistic "core" and "protective belt" of the Extended Synthesis. In this "Darwinian Pluralism" framework, as proposed by N. Eldredge and S.J. Gould, Hierarchy Theory should be at the centre of any further discussion about the revision and extension of the structure of evolutionary theory, as an interpretation of theoretical and empirical novelties with huge implications - like researches on macroevolutionary ecological patterns, Evo-Devo, epigenetics, multiple ways of speciation, and the role of structural internal constraints. Moreover, it should result useful also when we discuss the extension of evolutionary models in non biological fields, avoiding the application of just metaphorical and rhetorical forms of "ultra-Darwinism".

Emanuele SERRELLI[9]

Criticizing adaptive landscapes and the conflation between ecology and genealogy

Abstract: Disentangling ecological vs. genealogical dimensions is a core task of hierarchy theory in evolutionary biology. As Eldredge repeatedly epitomized, organisms carry out (only) two distinct kinds of activities: they survive, and they reproduce. At the organismal level, the organism stays the same whether we consider it ecologically or genealogically - yet, differences can occur in what features we consider relevant, and what fitness measurement we use. At higher levels, the two dimensions diverge, realizing different systems. Reproductive (deme) may not coincide with ecological (avatar) population. Further upwards, along the ecological dimension, higher-level systems are grouped by energy-matter interconnection, whereas, along the genealogical dimension, higher taxa are assembled by relatedness. In Dobzhansky's (1937) use of the adaptive landscape visualization (Wright 1932), all living species are imagined as distributed on adaptive peaks which correspond to ecological niches in existing environments. Peaks are grouped forming genera and higher taxa (e.g., "feline", "carnivore" ranges), and geographic speciation is figured out - like adaptation - as movement on the landscape. In criticizing Dobzhansky's landscape, Eldredge wrote that species actually do not occupy ecological niches; demes don't, either; avatars do. I point out that

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neighborhood and movement need to be conceived separately in genealogical and ecological spaces. Indeed, ecology should be further split in at least two spaces: geographic and phenotypic/adaptive. Movement in one space may in fact result in stability in the other(s). I also comment on the adaptive landscape: technical limitations prevent it from being coherently used above the population level, even though as a metaphor. Finally, I emphasize the partiality of any landscape - based on the choice of relevant features and fitness components - and interpret partiality as the way of approaching complex multi-hierarchical structure in evolution.

Ilya TËMKIN[10]

Nested Networks and Biological Diversification

Abstract: A comprehensive evolutionary theory requires a model of an all-inclusive structure of the natural world. The contemporary hierarchy theory provides an approach for tackling the dynamics of complex phenomena by viewing evolutionary patterns as emergent outcomes of processes occurring at different levels. It does not, however, address the nature of these processes and offer a general fine-grained model of the mechanisms by which they are integrated. Recent advances in network science revealed that a wide spectrum of natural processes could be described and studied in terms of complex networks. Striking structural and functional similarities of biological networks across hierarchical levels—from regulation of gene expression to ecological interactions—have major implications for evolutionary theory. The persistence and functional stability of complex biological networks resulting from common structural elements provides a perspective of viewing evolutionary phenomena as emergent synergetic effects of network dynamics at multiple hierarchical levels. The proposed expansion of the hierarchy theory of evolution to embrace the rising network theory offers a unified general approach to analyze evolutionary causality and a novel framework for generating testable hypotheses. In this view, biological diversification (a product of species origination and extinction) is regarded as a regional ecosystem-level phenomenon involving a cascade of network perturbations at different levels resulting in rapid ecosystem restructuring and accompanied by synchronous punctuated phenotypic evolution across multiple lineages. From a historical perspective, uniting networks and hierarchies into a single theoretical evolutionary framework reconciles the intrinsic formalist and external deterministic views of natural world, as well as makes irrelevant the false dichotomy between functional and historical sciences.

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