

What is the Hierarchy Theory of Evolution?

Biological systems are arranged hierarchically, with smaller units forming the components of larger systems: trees in a forest, cells in a body, organisms in a population, trophic groups in ecosystems, genes within chromosomes, within cells, within organs, within organisms, within populations, within species, within ecosystems. Hierarchy Theory of evolution is a theory of how biological hierarchies are organized, how they function, and how evolution takes place through them over time. 'Hierarchies' is a plural term in Hierarchy Theory, not only because hierarchical instances can be counted millions everywhere -- every organism or every local ecosystem is a hierarchical entity, therefore, it is a particular hierarchical instance. 'Hierachies' is a plural term because there are distinct kinds of hierarchies.

Proposed by eminent paleontologist and evolutionist Niles Eldredge since the mid-Eighties, the Hierarchy Theory of evolution provides a unifying approach to represent the complex multi-level structure of the organic world, and an explanatory framework for a wide range of natural phenomena. Hierarchy Theory identifies two main kinds, perhaps the only two that are really important in evolution. One is named 'economic' or 'ecological', and it is based on matter-energy transfers and ecological processes. The other is named 'genealogical' or 'evolutionary', and it is based on information and replication. The two hierarchies overlap at some point. For example, an organism is both an economic entity and a replicator, being part of ecological processes and also a fundamental element of a lineage. At other points, the two hierarchies are clearly distinct, for example a species is a genealogical entity that doesn't participate, as such, into any economic system. Even where the two hierarchies overlap, according to Hierarchy Theory, they are ontologically distinct, they interact in complex ways, and it is their interaction that brings about the patterns of evolution at all scales.

Niles Eldredge's fundamental intuition is therefore based on the non-coincidence and interrelation between ecology and genealogy, and their interactions in the so-called Sloshing Bucket model.

Hierarchy Theory and the Sloshing Bucket also suggest re-thinking concepts such as natural selection, species, and speciation that have always been part of evolutionary theory.

Eldredge has been elaborating the theory since the 1980s with various colleagues -- for example, initially, philosophers Stanley Salthe and Marjorie Grene -- giving rise to a network of scholars informally known as "The Hierarchy Group". Today the Group comprises, among the others, scientists like Dan R. Brooks, T. Ryan Gregory, William Miller III, Ilya Tëmkin, Bruce Lieberman, as well as philosophers and historians like Telmo Pievani, David Sepkoski, Emanuele Serrelli.

Hierarchy Theory is now at a crucial point of development. On the one hand, it needs to be systematized, because evolutionary thinking has not been assimilating its crucial intuitions that

would solve or at least reframe many long-standing theoretical problems. Think, for example, to the endless debate on multilevel selection, or to puzzling but crucial notions such as fitness or species or information. On the other hand, much work is still to be done on clarifying the two hierarchies: their nature, their general organization principles, the levels that compose them, all the processes that take place in their interaction, and their sufficiency in accounting for evolution. Some levels are particularly out of focus in the theory. The 'organism' level would benefit very much from the terrific advancements of biomedical sciences in conceptualizing organismal organization. As evolutionary biology advances with fields such as EvoDevo, phenotypic plasticity, comparative genomics, ecosystems and Earth evolution, work on Hierarchy Theory must become a priority: while the theory needs constant integration as biology proceeds, biology needs the theory -- the elephant in the room -- the 30-years old Hierarchy Theory of evolution.

Evolutionary fields of inquiry involved in the hierarchy theory

The Hierarchy Theory provides a single explanatory framework for integrating the tremendous recent advances in different specialized fields of biology, from elucidating the molecular basis of development, to human genome sequencing, to inferring the structure of the global tree of life. Speciation and extinction are here depicted as two sides of the same coin, as the latter represents the opportunity to give room to the former. Such a perspective permits to highlight and stress the importance of the occurrence of macroevolutionary patterns and processes. Hence adaptation and natural selection are two main concepts of evolutionary biology which the Sloshing Bucket Theory aims to reshape.

Genetic inheritance and variation, common descent and phylogeny are also some of the main biological fields of inquiry involved in the hierarchical discussion.

The Hierarchy Theory also allows fertile discussions in an integrated way of theoretical issues that are most debated, such as co-evolution, development, phenotypic plasticity, niche construction, genomic evolution, multiple channels of inheritance.

The role of a hierarchical approach in the extension and revision of the general structure of the Neo-Darwinian theory of evolution appears crucial.

Hierarchy theory and human evolution

The Hierarchy Theory is also able to provide deep insights about human evolution, such as the emergence of *Homo sapiens* both from a biological and cultural perspective (gene-culture co-evolution). In fact, according to the most recent discoveries in the field, ecology seems having

played a key role in promoting human macro-evolutionary pace, in particular influencing migration waves, geographic distribution areals and so improving the possibility of reproductive isolation and speciation.

This re-worked concept of speciation and, more generally, eco-genealogical diversification, seems to play a key role in the latest “inference to the best explanation” models of hominin evolution that integrate all the clues coming from paleontology, archaeology, molecular biology, and neuroscience.

The new models show three evolutionary phases closely intertwined with ecology: (1) 200 to 80 Kya: emergence of genetically and anatomically modern populations in Africa and first waves out of Africa to southwest Asia; (2) 80 to 60Kya: punctuated bursts of cultural innovation in Africa, with climate instability triggering demographic expansions and contraction; (3) 60 to 50 Kya: final wave of cognitively modern humans rapidly spreading in Eurasia and then Australia and Americas, broad hunting and extinction of mega-fauna and demographic substitution of all the other human species or forms.

The relationship between ecology and genealogy/genetics/evolution (i.e., the circulation of information) is interactive and bidirectional: the first phase is characterized by anatomic innovation and mainly by a neotenic trend in the genus *Homo* (reorganization of gene expression, new neural substrate, influences on social organization and communication, episodic expressions of symbolic behavior); the second phase shows the complete evolution of vocal trait that would have enabled fully articulated language, and the earliest evidence of symbolic behavior in Africa; and the third phase sees the branching and merging diffusion of modern complex languages and cultural diversities along with genetic information, by which we can today trace the globalization history of our species. According to the recent “serial founder effect” model, the decrease of genetic diversity in current human populations, highly proportional to the distance from Africa, could be explained by a sequence of genetic drifts produced by the movements and expansions out of Africa of such hunter-gathering bands.

Major change in the human ecological condition occurred during the First Agricultural Revolution ca. 10,000 years ago. It was a change in ecological circumstance, sharply brought into perspective when viewed through the prism of hierarchy theory. It is easy to show that hominin bands, up to and including the by-now nearly-extinct hunter-gathering bands (such as the San peoples of southern Africa), with their integration of ecological and reproductive functions, were nonetheless still members of their local ecosystems – utterly dependent, for example, on the productivity of the lands on which they lived, as well as their individual and collective skills of harvesting plant and animal resources. The invention of farming and animal husbandry effectively removed humans for

the first time from depending solely upon the resources afforded by their local ecosystems, and *Homo sapiens* became the first species whose local populations did not have ecological niches – and indeed were living outside local ecosystems. This condition underlies the nature of much of global human existence for the past 10,000 years or so.

Philosophical Features of the Hierarchy Theory

Depicting the biological world in a hierarchical structure permits to show properly how evolutionary biology is a 'Science of the Multiple Causes', just as Ernst Mayr said. The biological hierarchy is organized into nested levels of increasing dimension: genes, within chromosomes, within cells, within organs, within organisms, within populations, within species, within ecosystems. Each level can exert influences over entities occupying other levels and causal vectors run up and down the hierarchical levels. Matching this hierarchical structure with an evolutionary context displays a fundamental issue: whether selection or other processes of evolutionary significance can occur at different hierarchical levels and whether this can produce consequences of evolutionary significance at another hierarchical level. Processes occurring at a certain level can overflow that very level and produce significant effects at other, higher or lower, levels. This is what is called, in the hierarchical jargon, upward causation and downward causation.

An important terminological and conceptual distinction is the one between levels of selection and units of selection. The latter is the biological entity, such as an organism, a population or a gene, which can undergo selection processes. The former is the domain of biological organization occupied by a unit within the hierarchical structure.

Such a view of a multiplicity of causal factors occurring simultaneously within the hierarchical structure depicts a pluralistic and non-reductionist view not only for the causality in place, but also for the multiplicity of patterns at play, all of them capable of influencing evolution's outcomes. It is straightforward that a gene-centered view cannot fill in all the explanatory needs displayed in a hierarchical perspective, simply because the genetic level is just one of the main levels at play in the hierarchical structure.

Historical arrangement of the Hierarchy Theory

Darwin himself, already in *The Origin of Species* (1859), was concerned about the possibility that in some cases selection could operate at levels different from the organismic one. In *The Descent of Man* (1871), Darwin talked about a sort of 'community selection' between tribes referred to human evolution. Regarding the hierarchical structure of evolutionary theory, August Weismann (1834 –

1914), starting from his embryological works on somatic and germ-line cells, built the first truly hierarchical theory of evolution. After the Modern Synthesis the Hierarchy Theory came back of interest during the second half of the Twentieth Century, thanks to a renovated debate on group selection, thanks to the discovery of genetic neutralism by Motoo Kimura (1924 – 1994) and thanks to the precious works of paleontologists like Stephen J. Gould (1941 – 2002), Elisabeth Vrba and Niles Eldredge about speciation, macroevolution and paleobiology. Furthermore new studies about the major transitions in evolution and the multi-level selection theory stir the debate around the Hierarchical Theory in Evolutionary Biology.