

Bucket thinking: the future framework for evolutionary explanation

Pensamiento cubeta: el marco futuro de la explicación evolucionista

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ABSTRACT

The hierarchical interplay between ecology and genealogy is a fundamental ingredient for the most compelling current explanations in evolutionary biology. Yet philosophy of biology has hardly welcomed a classic fundamental intuition by palaeontologist Niles Eldredge, i.e. the non-coincidence and interrelation between ecology and genealogy, and their interaction in a Sloshing Bucket fashion. Hierarchy Theory and the Sloshing Bucket need to be made precise, developed and updated in light of an explosion of new discoveries and fields and philosophical issues. They also suggests re-thinking concepts such as natural selection, species, and speciation that have always been part of evolutionary theory.

KEYWORDS

EVOLUTION, ECOLOGY, HIERARCHY THEORY, SLOSHING BUCKET, HOMO SAPIENS

RESUMEN

La interacción jerárquica entre ecología y genealogía es un ingrediente fundamental de las más convincentes explicaciones de la biología evolucionista en la actualidad. Sin embargo, la filosofía

de la biología apenas ha acogido una intuición fundamental y clásica debida al paleontólogo Niles Eldredge, a saber: la no-coincidencia e interrelación entre la ecología y la genealogía, y su interacción a modo de cubeta rebosante. La Teoría de la Jerarquía y la de la Cubeta Rebosante necesitan mayor precisión, así como un ulterior desarrollo y actualización a la luz de la explosión de nuevos descubrimientos y campos y de cuestiones filosóficas. Siguiereen asimismo la necesidad de repensar conceptos tales como selección natural, especie y especiación, que han formado siempre parte de la teoría evolucionista.

PALABRAS CLAVE

EVOLUCIÓN, ECOLOGÍA, TEORÍA DE LA JERARQUÍA, CUBETA REBOSANTE,
HOMO SAPIENS

I. BIOGEOGRAPHY AND ECOLOGY IN EVOLUTIONARY EXPLANATION:

THE CASE OF *HOMO SAPIENS*

THE MOST RECENT MODELS OF HUMAN EVOLUTION (Pievani 2012) operate a massive integration among all the clues coming from palaeontology, archaeology, molecular biology, and neuroscience. They propose new solutions to some long-standing mysteries of human evolution, such as the so-called Palaeolithic Revolution (80-60Kya), but they also carry a methodological lesson: it is impossible to solve the mysteries of evolution without geographical reference and an intergenealogical look. That is to say: part of the sources of our incapacity of proposing plausible evolutionary hypotheses reside in an evolutionary thinking which is eradicated from geographical dimensions and ecological complexity.

I.1. FIRST BIRTH: HOMO SAPIENS AND ITS SPECIATIONAL CONTEXT

The speciation context of the birth of our species (200-80 Kya) has been pretty clear for many decades now. The first *Homo sapiens* made their appearance in a context of evolutionary experimentation triggered by climate change and local ecological conditions: in sub-Saharan Africa during the upteenth dry phase which coincided with the last Quaternary Ice Age. This phase is characterized, all through the hominid clade, by anatomic innovation, mainly by a neotenic trend, i.e., different modulation of gene expression regulating extended growth and developmental phases, contextual with the appearance of a new neural substrate, with apparent influences on social organization and communication, and episodic expressions of symbolic behavior. *Homo sapiens* was a small population with many shared traits in this context, and some identifying traits such as a tall and slim build, large skull and cranial capacity (1400cc),

good stone working skills and a longer development than those found in any other *Homo* (Bruner, Manzi & Arsuaga 2003).¹

But *Homo sapiens* was born a second time, i.e. with the beginning of cognitively modern humans, 80 to 60 Kya. This phase has always been described as the Palaeolithic Revolution or the «great leap forward», emphasizing the sudden and unprecedented appearance, throughout the areas of distribution of *Homo sapiens*, of all the evidence arguably related to cognitive modernity.² In fact, in the last decades very important pieces of evidence were accumulated. 75Ky, is the age of engravings and decorations found in South Africa, while new and extremely innovative behaviors in European Cro-Magnons, are much younger. Indeed it seems that we have a first «burst» of innovation in South Africa. Some studies even seem to support a degree of anatomical innovation in this same spatiotemporal context. Lieberman & McCarthy (2007) found a meaningful difference in speech physiology between the vocal tract of an early *sapiens* specimen (100Kya) from Israel, associated with Middle Palaeolithic stone tools, and the vocal tract of eight *Homo sapiens* specimens from the Upper Palaeolithic (40-10Kya), associated with more complex stone tools. Articulated language requires pre-linguistic competences concerning social learning and tool production (Lieberman 2006), but also a typical right angled vocal tract, i.e. an elongated vertical section (larynx, vocal cords, pharynx) as long as the horizontal section (palate to lips).³ Studies like Lieberman & McCarthy (cit.), if corroborated, would undermine the notion that modern humans did not change in their anatomy in the last 200Ky. At the same time, they would grant a crucial role to a slight change, in relation to *Homo sapiens*'s «the overall structure» (Lieberman, 2006) including ecological, behavioral, social, and demographic factors.⁴

1 Mitochondrial DNA data has been showing since 1987 that *Homo sapiens* differentiated in sub-Saharan Africa from the more ancient populations (Cavalli Sforza, Menozzi & Piazza 1994), possibly *Homo heidelbergensis* in the African version. Confirmation came from paleontological and archaeological data too.

2 One means of coping with this abruptness was the «exaptive hypothesis» about the emergence of cognitively modern humans: their cognition would imply a cascade functional reorganization with no anatomical innovation, triggered by a cultural innovation, probably language (Tattersall 1999). Sometimes the exaptive hypothesis has been considered saltationist and unexplanatory (e.g. Dennett 1995); on the other hand, some scholars thought that the great leap forward was an artifact of the lack of palaeontological and archeological evidence for that period (McBrearty & Brooks 2000, Henshilwood & Marean 2003).

3 Lack of this feature implies that *Homo neanderthalensis*, although possibly endowed with some morphological and genetic preconditions (hyoid bone and FOXP2 gene sequence), may have had only a basic or partial form of verbal language.

4 This would be an improved specification of the exaptive hypothesis which doesn't exclude (indeed, requires) natural selection and further change after the inception of a new func-

1.2. THE BIOGEOGRAPHICAL CRADLE OF A SOUTHAFRICAN FINAL WAVE

There is more evidence now, but the increased resolution geographical, not only temporal (allowing for a finer reconstruction of evolutionary stages). And the models of human evolution tell that geography could be the keystone for the interpretation of the fragmentary data about human evolution. Geography and genealogy are strictly related, and the inherited information bears traces of what happened in the geographical and ecological spaces of the past, although it is very difficult to find reliable causal connections between climatic changes, demographic fluctuations, and clues laid down in genetic diversity. The exceptionally low level of genetic diversity in our species –lowest than in any other primate (Kaessmann *et al.* 2001; Huff *et al.* 2010)– could be related to one or more population bottlenecks, i.e. drastic reductions in population numbers, we went through in our evolution. But how many, and when? Molecular data show a possible fall in *Homo sapiens* numbers around 70-75Kya, just in coincidence with a drop in global temperatures due to a «volcanic winter» caused by the catastrophic eruption of Toba on the Isle of Sumatra (Gathorne-Hardy & Harcourt-Smith 2003). Alternative hypotheses see a bottleneck 190-123Kya related to increased aridity in Africa, due in turn to changes in winds and rainfall. This hypothesis is interesting for what concerns South Africa, where the few *Homo sapiens* may have found coastal refuges in the Cape, leaving some archaeological evidence we are collecting today (Marean *et al.* 2007). A third bottleneck hypothesis emphasizes the multiple waves of emigration of *Homo sapiens* out of Africa: although our species left the African continent many times (the major three being 120-100Kya, 85-80Kya, and 60-50Kya) we would all be descendents of a Final Wave, which should have undergone a series of founder effects through its global diffusion (Deshpande *et al.* 2009). The genetic variance of any today's human population seems indeed inversely proportional to its distance from Africa (Ramachandran *et al.* 2005). The Final Wave would have been preceded by a phase of demographic expansion of the group to go: all mt-DNA lineages found today outside Africa descend from an African haplogroup called L3, and the youngest major African L3 haplogroup corresponds to an increase in population size 86-61Kya (Jacobs & Roberts 2009). The Final Wave, 60-50 Kya, is thus a further stage of this biogeographical story, where climate instability triggers demographic expansions and contractions, punctuated bursts of cultural innovation in Africa, and first waves of emigration out of Africa. This stage is the one where cognitively modern humans rapidly spread in Eurasia and then Australia and Americas, they perform broad hunting and

tion (Pievani & Serrelli 2011).

probably cause the extinction of mega-fauna and demographic substitution of all the other human species or forms.

*I.3. THE FINAL WAVE IN ACTION:
CAUSES AND CONSEQUENCES OF GEOGRAPHICAL EXPANSION*

But recent hypotheses bring ecogeography farther to the heart of the innovation that made the *Homo sapiens* of the Final Wave what they were. Jacobs et al. (2008) believe that local, African environmental changes (not the ones like Toba or draught listed before) produced repeated pulses of demographic expansions and contractions, influencing social networks and cultural innovation capacities in small groups of *Homo sapiens* during the Middle Stone Age in southern Africa. Symbolic behavior could have originated in such a complex scenario of evanescent cultures associated with little hunter-gatherer populations. In this context of punctuated and ephemeral innovations these researchers frame the two cultures of Still Bay (71-70Kya) and Howieson's Poort Points (65-60Kya), which were anomalies in the previous «great leap forward» story, but which are exactly included in the time span of the expansion of the L3 haplogroup (Jacobs & Roberts 2009). The alternation between phases of breakdown of social and economical networks and phases of demographic expansion and reconnection (with short-lived expansions out of Africa) would have been a crucial element of a constructive evolutionary loop between *Homo sapiens* and its environment. Another crucial element is bio-cultural innovation. An old and still valid idea (Atkinson, Gray & Drummond 2009) is that cultural innovation and behavioral complexity may translate into group competitive advantage by allowing for group cohesion, coordination, and efficiency. Language could have been a further «secret weapon» for the band that eventually performed the Final Wave –a story, according to Atkinson (2011), supported by the loss of phonemic diversity in languages proportional to the distance from Africa. But even here, researchers do not see monodirectional, linear causality from bio-cultural innovation to demographic expansion. Since small populations are notoriously a locus of evolutionary innovation, fragmentation could have allowed for the emergence of a group with bio-cultural characteristics, allowing in turn for geographical expansion. But, researchers say, population expansion and geographical dispersion may themselves have fed back into more innovations, including the Still Bay and Howieson's Poort Points (Jacobson & Roberts 2009).

I.4. HUMANS AND THEIR ECOLOGICAL CONTEXTS AFTER AGRICULTURE

Hominid 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 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 (Eldredge 1995b, 2000). The First Agricultural Revolution, ca. 10 Kya, was a major change in the human ecological condition: 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. But even agriculture didn't change the fundamental double framework –ecological and evolutionary– which is necessary to understand the sequences of events in our history. All the most if we consider that farmer populations became biodiversity producers as well as annihilators.

II. HIERARCHY THEORY AND THE SLOSHING BUCKET

The interplay between ecology and genealogy is a fundamental ingredient for many of the most convincing explanations of the history of life, including the most advanced models of human evolution. But how should the two dimensions be integrated in a coherent framework? It is well-known that ecology, as a scientific field with its own models and theories, has grown apart separated from evolution (Mikkelsen 2007, Matthews *et al.* 2011). On the other hand, micro-evolutionary biology tends to embed a simplified account of the environment, boiled down to selective pressures and other factors. Just think to the schemes that are currently referred to as «recipes» of natural selection (Godfrey-Smith 2009): Lewontin's classical «variation-inheritance-fitness differences» (1970), the replicator-vehicle distinction (Hull 1980, Dawkins 1976) recently updated by Griesemer (2000), other formulations based on phenotype heritability (used, e.g., in Okasha 2006) or more articulated concepts involving the definition of a Darwinian population (Godfrey-Smith, *cit.*). All these descriptions are intra-genealogical and formalize the environment, if anything, as a bending factor to some organismal or population variables. Evolutionists concerned with macroevolution are those who are more used to see the relationships between, on the one hand, palaeoenvironments and their dynamics, and, on the other hand, phylogenetic branching and evolutionary innovation. Among them, Niles Eldredge proposed one of the most coherent frameworks to reveal the connection between ecologies and genealogies.⁵

II.1. BIG DISRUPTION, BIG CHANGE: THE SLOSHING BUCKET MODEL

A fundamental passage of Eldredge's thinking concerns the recognition that events in the history of life have very different magnitudes. For Eldredge,

5 See, e.g., Eldredge (1984, 1985, 1986, 1992, 1995, 1999, 2003).

evidence from geology, palaeoecology, and palaeontology supports a Shloshing Bucket model of evolutionary stability and change (Eldredge 2003): in the history of life, the magnitude of ecological perturbations match the extent of evolutionary change. *Localized* ecological disruptions often result in the re-establishment of similar local ecosystems, by recruitment of conspecifics that still live outside the affected area. On the grandest scale, *global* environmental disruption is coupled with the disappearance of larger-scale taxonomic entities, and, over periods of millions of years (typically 5-10 My), modified species derive from taxa that survived the extinction event. For Eldredge the most interesting situation is the intermediate one, where *regional ecosystems* are disturbed: the fossil record shows that most speciation events take place as a consequence of regional ecosystemic collapse and multiple extinctions of species across different lineages, and for Eldredge speciation is basically what brings about evolutionary genetic change in the history of life.

There are events of different magnitudes also in the human evolution model presented above. The dry phase in the last Quaternary Ice Age corresponds to an important period of evolutionary innovation all through the hominid clade, and very likely over other vertebrate clades represented in Africa. This genealogical transversality leads us to a fundamental decoupling: any biogeographical setting comprehends representatives of *many* lineages, therefore ecological events will impact all of them transversally; on the other hand, lineages of relatives are usually distributed through *many* different places and environments, hence we can rarely see them properly as parts of an ecosystem (a habit which is, instead, very widespread). The strong habit of conflating ecology and genealogy is exemplified by the fact that hierarchical representations like the following are accepted without a blink: organism–population–species–ecosystem–biosphere.⁶ Yet, putting species and ecological niches in the same hierarchy is a logical absurdity. As Eldredge stated clearly many times (e.g., 1995a), local populations occupy ecological niches, while species don't: they are featured in many ecosystems within their distribution area. Even at the scale of local populations, ecological groups and reproducing groups (demes) often do not coincide. A local population can play a somehow unitary ecological role while being divided in non-mutually-breeding sub-groups. Ecology and genealogy are

6 Indeed we find a similar grouping all over the place in the works of the founding fathers of modern evolutionary biology. Dobzhansky (1951), for example, wrote: «the ecological niche occupied by the species “lion” is relatively much closer to those occupied by tiger, puma, and leopard than to those occupied by wolf, coyote, and jackal. The feline adaptive peaks form a group different from the group of the canine ‘peaks’. But the feline, canine, ursine, musteline, and certain other groups of peaks form together the adaptive “range” of carnivores, which is separated by deep adaptive valleys from the “ranges” of rodents, bats, ungulates, primates, and others» (1937/1951, p. 10).

non-coincident but interrelated. In human evolution, localized events such as African climate fluctuations may have caused iterated social and geographical fragmentation, with no speciation but with intraspecific modifications.⁷ These innovations may have brought about an exceptionally expansive migratory subpopulation, that began modifying its own genetic makeup by settling in new territories (founder effects, genetic gradients), also assisting to the extinction of its closest relatives in the reached territories.

*II.2. TWO KINDS OF HIERARCHIES:
ECOLOGICAL/ECONOMIC, AND GENEALOGICAL/EVOLUTIONARY*

The two «walls» of the Bucket are, for Eldredge, two hierarchies:⁸ the *ecological* hierarchy and the *genealogical* hierarchy, respectively.⁹ The core intuition running through the various scales of the Bucket is that organisms are part of at least two different kinds of systems: (1) *matter-energy* transfer systems, where organisms are parts of local populations that in turn are parts of nested ecosystems; (2) *genetically-based* information systems, where organisms are parts of local breeding populations that in turn are parts of species, which belong to historical lineages –genera, families, orders, etc.:

The clue to unravelling the evolutionary consequences of interactions [between ecosystems and species] derives from the observation that organisms seem to be both energy conversion machines and reproducing ‘packages’ of genetic information. As such they are integrated simultaneously into two largely separate, but interacting kinds of general systems (Eldredge 1986, p. 351).

Seen as matter-energy transfer systems, organisms are parts of «avatars» (Damuth 1985) that in turn are parts of local ecosystems. The economic roles played by such populations are what constitute ecological niches. Local ecosystems are parts of regional systems, a geographic mosaic of matter-energy transfer systems that together constitute the global biosphere. Seen as genetically-based information systems, or as units making more of themselves, organisms are parts of «demes» up through the Linnaean Hierarchy. Eldredge stressed that, while evolutionary theory has legitimately focused most on genetic processes and the

7 Including, for Lieberman and McCarthy (2007), also those involving the completion of articulated language.

8 Niles Eldredge (e.g., 1986) adopted Hierarchy Theory as an approach to understanding the evolutionary process. The birthdate of Hierarchy Theory can be located in the 1980s when, in the context of complexity theory, several scientists (e.g., Allen & Starr 1982) and thinkers (e.g., Salthe 1985) began exploring in detail the nature of hierarchical systems. Hierarchy Theory uses a relatively small set of principles to keep track of the complex structure and behavior of systems with multiple levels such as social systems, physical and biological structures, and biological taxonomies.

9 An interesting work on a similar distinction is Caponi (2012).

formation of genetic lineages, evolution does not occur in a vacuum: rather, it is what takes place inside matter-energy transfer systems that determines, in large measure, the patterns of stability and change in genetic systems that we call «evolution».

The fact that global environmental disruption coincides with mass extinctions (Raup & Sepkoski 1982, 1984, Eldredge 1991), i.e. the hardly selective disappearance of higher-rank taxonomic entities, can be evident also to non-specialists of macroevolution. But, for Eldredge, *at all scales* the interplay of the economic and the genealogical hierarchies is a crucial way of framing the explanation of the patterns of biological systems and their histories. Ecological disruptions with different pulse, pace and scope have *corresponding effects* on matter-energy systems on different scales, and the Sloshing Bucket theory of evolution states very generally that evolutionary change is driven by ecological dynamics that have repercussions on the information stored in the genealogical hierarchies. Eldredge's proposal is thus a flipover of the traditional primacy given to genealogy over ecology, although the genealogical hierarchy is active in offering the dynamics for conservation and innovation that enter in the ecological arena. The innovative load of this thinking and, at the same time, its scarce penetration in common thinking, is exemplified by the standard presentation of core concepts like natural selection and speciation.

II.3. NATURAL SELECTION AND SPECIATION IN THE SLOSHING BUCKET: REINVENTING EVOLUTION

Natural selection is a telling example of how Hierarchy Theory can reformulate the most basic concepts of evolutionary theory. Natural selection is an ecological process, whose «raw recruit» is the intra-populational, inter-individual variation of ecologically relevant traits provided by the working of the genealogical hierarchy. Although organisms are units that reproduce *and*, at the very same time, units that appear on the ecological stage, conceptualizing natural selection requires a distinction between the nested systems of inheritance (family, deme, species, genus etc.) and the nested ecological systems (the avatar with a local ecological role, the local multi-species ecosystem, and regional ecosystem, up to the biosphere). Standard accounts of natural selection instead translate ecological differences automatically into units of reproductive success, thus conflating the processes that Eldredge's framework wants to disentangle. Thousands of examples would illustrate such an opacization of both the phylogenetic context and the ecological rhythms and dynamics. One for all: D.S. Wilson's (2010) argument that in human evolution projectile throwing was converted into social surveillance, allowing for the suppression of intra-group selection in favor of inter-group selection, and yielding an evolutionary major

transition.¹⁰ Reconstructions like Wilson's try and stand without reference to the multispecies and fluctuating context we presented above, as if internal variation and an absolute measure of fitness could be able to account for evolutionary change. Reflecting on the actual interaction between ecology and genealogy is the challenge cast by Eldredge and by the evolutionary scenarios that await for being explained, albeit more complex and conjectural.

Hierarchy Theory clashes also with traditional presentations of speciation that commonly depict *one species at a time*, and classify speciation events as allopatric or sympatric, and then for example peripatric or parapatric, therefore *on a geographical basis* (after Mayr 1942). In light of Hierarchy Theory, both these habits are wrong. First, by «geographic speciation», we mean not much an eco-geographical event, but rather *one* of the possible genealogical *consequences* of ecological barriers, i.e. the outcome of a multiplication of genealogical entities at the level of species within instances of the evolutionary hierarchy. As Gavrilets (2010) pointed out, a geographical taxonomy of speciation is silent about what, if anything, happens *in* the genealogical hierarchy, for example about the kinds of genetic, morphological or behavioral «uncoordination» that yield reproductive isolation. A new genealogical taxonomy of processes of diversification is possible. Second, geographic barriers impact *many* species at once: ecological events which arguably trigger speciation are cross-phyletic. A proper re-description of geographic speciation should contextualize the phenomenon in the scenario of ecological systems (ecosystems and, at a macroevolutionary scale, faunas or biotas). Sometimes speciation can be adaptive,¹¹ but the important thing is that adaptation –usually seen from an intra-populational point of view as well– should be described in the context of ecological reassortment and reshaping of communities.

II.4. PHILOSOPHICAL ISSUES IN HIERARCHY THEORY

What work needs to be done on Hierarchy Theory? Eldredge's series of books and papers progressively developed and revised details such as the number of levels, acceptable entities, and processes, and this is a still much open enterprise. On the other hand, the work demonstrated the robustness, flexibility, and generality of the core intuition –the «unity in diversity» of the genealogical and the ecological dimensions– which is orthogonal and beyond the particular

10 «The reason that we are so unique among primates is that our ancestors became the primate equivalent of a single organism or a social insect colony» (Wilson, cit.).

11 A critical assessment of the relative frequency of adaptive speciation and of other relative frequencies require methods to compare very different taxa that are distantly related. Many studies, from time to time, try to overcome these methodological obstacles in order to obtain these important estimates concerning evolution as a process.

and contingent debates that have emerged in the last 30 years in evolutionary theory, such as:

1. *The ontological status of levels in the hierarchies*: do the two hierarchies exist as «things out there»? If not, they are an epistemological device, in which case their ontology would be variable, for example the levels will have to be demarcated from time to time according to epistemological needs. Similar positions are brought forth for both the phylogenetic hierarchy (e.g., Ereshefsky 1997) and the ecological hierarchy (e.g., Potochnik & McGill in press).
2. *The multiple species notions*: here we used the biological concept of species (a level in the genealogical hierarchy), with no necessary link with the individuality thesis. But even so, the biological concept of species is not the only one (Coyne & Orr 2004, Wilkins 2011), and it doesn't apply equally well to all life (O'Malley & Dupré 2007, O'Malley 2010).
3. *The requirements for individuality in evolution*: are the entities found at different levels of each hierarchy individuals? And in which sense? Despite the historical role of Eldredge and colleagues in exploring the individuality thesis in evolution (e.g., Hull 1980, Gould 2002, Wilson & Barker 2013), mainly through the idea of species selection (see Jablonski 2008), there doesn't seem to be a necessary commitment to the individuality thesis in Hierarchy Theory for any particular level.
4. *The units and levels of selection*: does selection happen among genes, or species, or other units beyond the organism? Hierarchy Theory allows for the now well-studied phenomenon of multi-level selection (Keller 1999, Okasha 2006), but also for other processes that are peculiar to different magnitudes and levels of the two hierarchies as Gould articulated finely in his latest work (2002).
5. *The tempo of evolution*: the Slushing Bucket theory is undeniably tied to a punctuated equilibria view of evolution (Eldredge & Gould 1972, Gould & Eldredge 1977, Gould 2002). Eldredge often argues that nothing interesting happens in evolution (therefore, stasis) without relevant disruptions in the ecosystems (punctuations). It is true as well that the Slushing Bucket accomodates events of many scales, including natural selection in stable environments. The relative frequencies and incidences of happenings of different magnitudes remains partly open (Eldredge *et al.* 2005), and so does a complete account of their causal patterns.

6. *Emergence, upward and downward causation, and reductionism among levels* are philosophical debates touched by the Hierarchy view, and probably necessary for clarifying what kind of scientific explanation is actually being proposed, and what are its ontological implications and requirements (see, for example, Craver & Bechtel 2006, Johnson 2010, Okasha 2011, Baetu 2011).

The list could grow a lot, touching e.g. the implications of Hierarchy Theory for taxonomy and systematics, or for the balance between adaptive and non-adaptive evolution. Many of these debates were heated in the 1980s and, not by chance, are still open today. Hierarchy Theory, albeit born in that culture ground, is not automatically committed to any position in every single debate. Rather, in many cases it can provide a framework for an answer. For example, it makes the question *whether macroevolution is causally distinct from microevolution* obsolete, by operating an irreversible unification confirmed by the contents of the most advanced natural histories (first of all, that of our species) and by their methods, integrating more and more precise palaeoclimatic, palaeogeographical intergenealogical data, molecular phylogeny and diversity studies. Adaptive and exaptive stories are reintegrated, but they are not any more confronted only with neontological data, recent environments, and rarefied, imagined, delocalized, adimensional ecological contexts supporting just-so stories.

III. CONCLUSION

When philosophers, theorists, and working scientists think about evolution, they often do so by means of models based on inheritance. Natural selection, for example, is quantified as selective pressures, intended as coefficients directly influencing reproductive outputs, or summaries of the influences on reproductive outputs. Ecology therein is often seen as the circumstancy of evolution, a source of perturbations and influences which is accurately reflected, translated into units of reproductive output. Yet contemporary explanatory models of biological evolution, for example those that are emerging for *Homo sapiens*, show that a much much better understanding of the constructive interaction between two independent domains –the ecological and the genealogical– is required not only to account for quintessentially macroevolutionary events such as mass extinctions, but also for smaller-scale happenings such as speciations and intra-specific evolutionary innovations. The huge frequency of utterly inheritance-centric philosophical works on natural selection seems, in this light, an unmistakable symptom of theoretical inertia. Bucket Thinking could reflect the way in which the best evolutionary explanations are built today, and at the same time aid the explanation by laying down and relating the researches that are being conducted in different fields (e.g. from population genetics to palaeon-

tology, from ecosystem ecology to developmental biology). Bucket Thinking is also a way of reframing many classical problems, such as multi-level selection, individuality, or even reductionism or emergence. This doesn't mean that Hierarchy and the Bucket are free of their own epistemological and methodological problems. On the contrary, what we suggest is precisely a critical philosophical discussion more deep than the one that has been deserved until now to these potentially fruitful ideas. Hierarchy Theory asks to be developed and updated in light of an explosion of new discoveries and fields, e.g., EvoDevo, lateral gene transfer and the charge of zoo-centrism pending on evolutionary theory (O'Malley 2010), network theory, genomics. But the dual Hierarchy Theory is also a way of re-thinking and re-framing concepts that have ever been present in evolutionary theory, like natural selection itself, or species and speciation, as we have seen here.

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