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SYNTHESIS PAPER

Hierarchy Theory of Evolution and the Extended Evolutionary Synthesis: Some Epistemic Bridges, Some Conceptual Rifts

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Abstract Contemporary evolutionary biology comprises a plural landscape of multiple co-existent conceptual frameworks and strenuous voices that disagree on the nature and scope of evolutionary theory. Since the mid-eighties, some of these conceptual frameworks have denounced the ontologies of the Modern Synthesis and of the updated Standard Theory of Evolution as unfinished or even flawed. In this paper, we analyze and compare two of those conceptual frameworks, namely Niles Eldredge's Hierarchy Theory of Evolution (with its extended ontology of *evolutionary entities)* and the Extended Evolutionary Synthesis (with its proposal of an extended ontology of *evolutionary processes)*, in an attempt to map some epistemic bridges (e.g. compatible views of causation; niche construction) and some conceptual rifts (e.g. extra-genetic inheritance; different perspectives on macroevolution; contrasting standpoints held in the "externalism–internalism" debate) that exist between them. This paper seeks to encourage theoretical, philosophical and historiographical discussions about pluralism or the possible unification of contemporary evolutionary biology.

Keywords Hierarchy Theory of Evolution · Extended Evolutionary Synthesis · Niche construction · Unfinished Synthesis · Macroevolution · Reciprocal causation

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> "(…) the problem with contemporary evolutionary theory is not that its essential neo-Darwinian paradigm is incorrect. The problem is that the consistency argument of the synthesis (…) is itself troubled. That argument says that the core neo-Darwinian paradigm (the theory that deals with the origin, maintenance, and modification of within-population genetic structure) is consistent with all other known evolutionary phenomena. This credo, innocuous and undeniable as it is, has been expanded to mean that the neo-Darwinian paradigm of selection plus drift, are both necessary and sufficient to explain all other known evolutionary phenomena. My position here, and the position of all other doubters of the completeness of the synthesis that I know of, is simply that the neo-Darwinian paradigm is indeed necessary—but is not sufficient—to handle the totality of known evolutionary phenomena. And it may not even be necessary to explain certain particular phenomena. It is thus not a matter of either/or"
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> Niles Eldredge (1985, p. 119)

Unfinished Ontologies of the Modern Synthesis: The Hierarchical Structure of Nature and the Neglected Processes in Evolutionary Thought

Written almost 35 years ago, the words of Niles Eldredge that we chose as our epigraph still resonate in the contemporary landscape of evolutionary biology (see Laland et al. 2014; Love 2017). As has been claimed many times (e.g. in Wagner 2014), the ontology and language of population genetics, the explanatory heart of the Modern Synthesis (MS), are far too limited and abbreviated to capture the richness of life. The consistency argument represented a pivotal desideratum in the early writings of the architects of the Modern Synthesis (Gould 1982; Beatty 1986; see also Mayr 1982), but it soon grew into an incomplete account of the 'furniture' of the biological world (Eldredge 1985). To use the words of the historian of biology William Ball Provine, the MS entailed both a "synthesis" (chiefly of Mendelian genetics, natural selection and "population thinking"[1]) and a "constriction" (Provine 2001). According to some traditional historiographies (see Futuyma 2015), such constriction or exclusion can be understood (and even excused) by putting into the limelight the state of evolutionary discourse in the early twentieth century (see Simpson 1944; Bowler 1983; Reif et al. 2000): the theory of natural selection was the subject of many negative assessments and major disparagement in Europe, the United States and other parts of the world in the so-called "eclipse of Darwinism". The architects of the Modern Synthesis had to stand out and fiercely shield the causal primacy of natural selection acting in particular populational contexts, in an attempt to explain phenotypic change, reproductive isolation, the gargantuan problem of the 'origin of species' and, by extrapolation, the macroevolutionary patterns of biodiversity. For Eldredge (1985), the purview of the MS limited its attention to only a few (ontologically real) biological entities involved causally in the evolutionary process: genes, organisms, demes and species (monophyletic taxa of higher taxonomic rank, for instance, were dimly appreciated); whereas ecological entities (e.g. populations as actors in the conversion and transfer of matter and energy, communities and regional biotas) were overlooked altogether. Eldredge yielded an *ontological argument* to challenge the explanatory sufficiency of the Modern Synthesis: "in order to use the neo-Darwinian paradigm to explain everything, we must stress the existence of some biological entities while ignoring (even denying) the existence of others" (Eldredge 1985, p. 119). In the eyes of that famous American paleontologist, what evolutionary biology needed in 1985 was a revised ontology (see also Hull 1980) of evolutionary entities and a subsequent restructuring of evolutionary theory. As Eldredge contended, an extended ontology could present an alternative but more truthful description of the organization of nature: a *hierarchical* structure. "Genes, organisms, demes, species, and monophyletic taxa form one nested hierarchical system of individuals that is concerned with the development, retention, and modification of information ensconced, at base, in the genome. But there is at the same time a parallel hierarchy of nested ecological individuals —proteins, organisms, populations, communities, and regional biotal systems, that reflects the economic organization and integration of living systems. The processes within each of these two process hierarchies, plus the interactions between the two hierarchies, seems to me to produce the events and patterns that we call evolution" (Eldredge 1985, p. 7). Thus, the Hierarchy Theory of Evolution (HTE) was born,[2] as a formal embodiment of the claim that evolution is probably a more complex affair than the MS would have us believe (as explicitly stated in Eldredge 1985), adding an *extended ontology of evolutionary entities* to the field of evolutionary biology (for a history of the so-called "paleobiological revolution" in which the HTE sprouted, see Sepkoski 2012; recently, the HTE has been updated with the framework of network theory, see Tëmkin and Eldredge 2015; Tëmkin and Serrelli 2016).

Since the advent of the MS, the field of evolutionary biology has continued to incorporate new theoretical and empirical findings (e.g. neutral theory of molecular evolution; inclusive fitness theory), covering a broader range of phenomena with refined explanations (Laland et al. 2015). However, new contentious developments have been forcibly accommodated and interpreted with undisputable agreement to the core assumptions of the original MS (Laland et al. 2015; see also Pigliucci and Müller 2010a). Historically, from the onset of the second half of the twentieth-century up to present times, several challenges to the MS have surfaced from multiple paleontological and neontological trenches, calling either to expand the standard theory (e.g. by recognizing the action of selection at different levels), extend it (by integrating unrecognized meaningful processes and fields of inquiry), or replace it altogether with a whole different framework (Depew and Weber 2013). For the proponents of the Extended Evolutionary Synthesis (EES), the narrow and "gene-centric" stance of the MS [or, more precisely, of what has come to be the updated "Standard Evolutionary Theory" (SET) in the twenty-first century] fails to capture the "full gamut of processes that direct evolution. Missing pieces include how physical development influences the generation of variation (developmental bias); how the environment directly shapes organisms' traits (plasticity); how organisms modify environments (niche construction); and how organisms transmit more than genes across generations (extragenetic inheritance)" (Laland et al. 2014, p. 162). According to its detractors, the standard interpretation of these phenomena underestimate its evolutionary implications: too much causal significance is granted to

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[1] We should stress that this historiographic account is not exempt of criticism. Two critical appraisals, among many others, are found in Amundson (2005) and Delisle (2011).

[2] However, in his recent book *Eternal Ephemera: Adaptation and the Origin of Species from the Nineteenth Century Through Punctuated Equilibria and Beyond*, Niles Eldredge (2015) claimed that the HTE is much older: it goes back to the early decades of the nineteenth century, with the pioneering contributions of Jean-Baptiste Lamarck and Giambattista Brocchi, among others (see also Eldredge 2016).

genes and selection, while constructive developmental processes that create novel variants, bias selection, contribute to heredity, and generate adaptive fit are belittled (Laland et al. 2015). Some of these processes, it has been claimed, were neglected until recently by the mainstream strand of evolutionary thought (see the case of ‘niche construction’ in Odling-Smee et al. 2003). The EES construes those processes as rightful evolutionary causes, whereas the orthodox evolutionists regard them as mere outcomes of evolution. From that standpoint, the EES sees an incomplete ontology of evolutionary processes in the SET. The EES, as a conceptual framework that emphasizes organismal causes of development, inheritance and differential fitness, the role of constructive processes in development and evolution, and reciprocal representations of causation, delivers an *extended ontology of evolutionary processes*, including those that generate novel variants, bias selection, modify the frequency of heritable variation and contribute to inclusive transgenerational inheritance (see Laland et al. 2015).

Contrasting the two cases (i.e. the Hierarchy Theory of Evolution and the Extended Evolutionary Synthesis) of assertions about the unfinished ontologies of the Modern Synthesis (and the updated SET) brings to mind a particular insight. At first blush, it seems that the correspondent extended ontologies of the HTE and the EES are, to a certain extent, complementary: the HTE provides an extended ontology of *evolutionary entities* and the EES proposes an extended ontology of *evolutionary processes*. Will a systematic analysis of the premises, core assumptions and conceptual architectures of both the HTE and the EES support or impugn this gross intuition?

Extended Ontologies in the Contemporary Landscape of Evolutionary Biology: A Road Towards Unification?

A few years ago, Eldredge (2008, p. 10) stated that “(e)volutionary biology is a notoriously diffuse field of scientific inquiry”. The discipline seems to comprise a plural landscape (surely, some biologists would prefer to call it a ‘befogged panorama’) of multiple co-existent conceptual frameworks and strenuous voices that disagree on the nature and scope of evolutionary theory (e.g. Oyama 2000; Kirschner and Gerhart 2005; Dieckmann and Doebeli 2005; Lynch 2007; Laubichler 2010; Wagner 2011; Winther et al. 2013; Nei 2013; Jablonka and Lamb 2014; Laland et al. 2014, 2015; Futuyma 2015; Pavličev and Wagner 2015; Pievani 2016a; Eldredge et al. 2016; Welch 2017). Thus, a crucial question arises: *what exactly is evolutionary biology in the twenty-first century?* It has even been contested that evolutionary biology should be portrayed as a single enterprise at all (see Serrelli and Gontier 2015 for thought-provoking questions). In this context, we wonder if epistemological pluralism should be embraced for evolutionary biology. Is the unification of this scientific field attainable? Is it something desirable (heuristically or epistemologically) and worth-pursing in the future? If so, what kind of framework could take up the colossal task?

In recent years, the Hierarchy Theory of Evolution has been depicted as a promising candidate to achieve that goal: Eldredge (2008) claimed that the meta-pattern of relationships between the ecological and the genealogical hierarchies is a putative framework for the theoretical ‘‘unification’’ of evolutionary biology. Pievani and Serrelli (2013) argued that the HTE allows re-thinking and re-framing protracted concepts of evolutionary theory (e.g. natural selection; species; speciation), and that the hierarchical interplay between ecology and genealogy (i.e. an interrelation in a “Sloshing Bucket” fashion; for an outline of this model, see Eldredge 2003) is and will continue to be a fundamental ingredient for the most compelling explanations in evolutionary biology; for philosopher of biology Telmo Pievani (2016a), an important theoretician of the HTE, this framework is a good example of a “meta-theory” that could integrate the sum of the observed evolutionary patterns (of small-, medium- and large-scale evolution) into a global and coherent structure. On the other hand, the Extended Evolutionary Synthesis is gaining ground in evolutionary biology: in 2016, a major grant was awarded to an interdisciplinary team of over 50 international scholars, with Kevin Laland (University of St Andrews, Scotland) and Tobias Uller (Lund University, Sweden) as the project leaders, for a three-year research program to “put the predictions of the extended evolutionary synthesis to the test” (see http://synergy.st-andrews.ac.uk/ees/the-project/). Moreover, researchers from different fields are embracing the EES as a working framework to deliver integrative explanations (see the cases of physiology in Noble et al. 2014; psychology and human cognition in Stotz 2014; sociocultural evolution in Blute 2015; biochemistry in Vianello and Passamonti 2016; biological anthropology in Fuentes 2016 and Vergara-Silva 2016; language evolution in Suman 2016; and plant domestication in Piperno 2017).

It is clear that the HTE and the EES are two important frameworks in the contemporary landscape of evolutionary biology. Are their extended ontologies complementary, or could they be easily linked together? Could they merge into a unique framework? In that regard, Pievani (2016b) asserted the following: “Evolutionary biology itself is an evolving scientific discipline, demanding for pluralistic explanatory models. Key concepts, advanced by the extended synthesis supporters, such as reciprocal causation (Laland et al. 2015), or catching the constructive relationship between the ecological environment and organisms’ behavior and development, could perfectly match with the multilevel framework proposed by hierarchy theory” (p. 363; emphasis added by us). We can then ask: Is that potential match so "perfect"? The objective of the rest of this paper is to outline some of the epistemic bridges and conceptual rifts that exist between the HTE and the EES, in the interest of future debates and thorough appraisals, both scientific and philosophical, about the 'unification' or pluralism in evolutionary biology.

Epistemic Bridges Between the HTE and the EES: Reciprocal/Multilevel Views of Causation, the 'Reinvented Organism' and Niche Construction

Reciprocal/Multilevel Views of Causation

In the last decades, several arguments called into question the adequacy of traditional causation schemes in evolutionary biology (reviewed in Martínez and Esposito 2014); some of those arguments focused on the necessity to reassess the famous dichotomy of proximate/ultimate causes, and others urged to complement the 'bottom-up' causal model with a 'top-down' approach. Specifically, some proponents of the EES dissent with Ernst Mayr's clear-cut distinction of proximate and ultimate causes (see Mayr 1961). For them, Mayr's heuristic dichotomy has proven problematic because it builds on a deterministic (gene-centric) view of development that led to the widespread belief that ontogenetic processes are irrelevant to evolutionary questions (therefore, unsuccessful to explain the origin of characters and evolutionary novelties) (Laland et al. 2011, 2013). Mayr's dichotomy disregards the fact that proximate mechanisms contribute to the dynamics of selection (Laland et al. 2011, 2013). Laland and collaborators (2011, p. 1516) make an interesting claim for historians and philosophers of biology to ponder: "It would seem that the manner in which biologists think about causality has acted like a metatheoretical conceptual framework to stabilize the dominant scientific paradigm". According to this view, Mayr's unidirectional characterization of causation paves the way for simplistic cause-effect explanations rather than focusing on broader trends, feedback cycles, or distributed causal influences throughout biological systems; this dichotomy forged artificial divisions within evolutionary biology and between the field and adjacent disciplines, and obstructed several contemporary debates in biology (Laland et al. 2011, 2013). In its place, these authors and other colleges advocate for a reciprocal view of causation, where developmental processes, operating through developmental bias and niche construction, co-construct with natural selection the organism-environment complementarity, and affect the direction and rate of evolution (Laland et al. 2015 for a critical assessment of reciprocal causation, see Svensson 2017). Additionally, several critiques to the reductionist assumptions preeminent in evolutionary biology have pinpointed the incompleteness of the bottom-up approach to biological causality (i.e. departing from molecules to ecosystems) (Martínez and Esposito 2014). For instance, Gilbert and Sarkar (2000) have defended an organicist stance where bottom-up and top-down approaches must be deployed conjointly to realistically attempt to explain the complex ontology of biological phenomena. Top-down (or downward) causation refers to the idea that "in a hierarchically structured system, causal influence may on occasion run from whole to part, i.e. down to the hierarchy" (Okasha 2011, p. 49).

These discussions on alternative schemes of biological causality are relevant to philosophical assessments of the HTE. Eldredge (1985) pointed out that the interactive nature of the various levels in the inclusive hierarchies encompassed in the HTE (i.e. genealogical and ecological) entails both upward and downward causation, which transcend the effects between the individuals of one level and their nearest (higher and lower) neighbors. Pievani (2016a) stressed that events produced at the highest level of the genealogical hierarchy can impinge downwards to lower levels, or conversely, causality can be propagated upwards. For the HTE, "in biological systems, a pair of adjacent levels comprises a dual control system, where the interactions of entities at a lower level establish initiating conditions (upward causation) and the interactions of entities at a higher level exert constraints, or determine boundary conditions (downward causation)" (Tëmkin and Serrelli 2016, p. 22).

The views of causation espoused by the proponents of the EES and the HTE are both 'reciprocal' *sensu lato*. The EES acknowledges causal co-determination (reciprocity) in the pairing of "developing organism-environment" and also the causal flow "both upwards from lower levels of biological organization, such as DNA, and from higher levels downwards, such as through tissue- and environment-specific gene regulation" (Laland et al. 2015). The HTE grants the existence of topward and downward reciprocal flow of causation as well (see Pievani and Serrelli 2013; Pievani 2016a). This is the first epistemic bridge we have detected between these frameworks: *compatible views of causation*. Both frameworks share the recognition of the reciprocal flow of causality (upwards and downwards), and, furthermore, what brings them closer is their rejection to the exclusively linear view of causation of the MS.

Multilevel causation, which is potentially a more inclusive framework to rethink causality in evolutionary biology, was proposed by Martínez and Esposito (2014) on the basis of the pioneering work of Donald Campbell (1974; see also recent discussions in Bertolaso and Buzzoni 2017). This concept takes into account all the mechanisms of causal determination and co-determination (i.e. feedback loops and reciprocal causation *sensu stricto*, as the latter has been defined in Laland et al. 2013), multiply directed (bottom-up and top-down), "(…) that occur between entities and events at different levels of organization, and that connect different time scales" (Martínez and Esposito 2014, p. 213). If both the EES and the HTE were to embrace a multilevel view of causation, the epistemic bridge linking them would become even stronger.

The 'Reinvented' Organism

In a recent essay entitled "Reinventing the Organism: Evolvability and Homology in Post-Dahlem Evolutionary Biology", the evolutionary biologist Günter P. Wagner (2015) put forth a different historiographical narrative, compared to the one in Eldredge's 1985 book (see Sect. 1), of what constituted the ontology of evolutionary biology from the inception of the MS to the early eighties. For Wagner, the ontology of real and valuable entities was restricted to genes (including its material basis, DNA, and its variants, alleles and haplotypes), populations (as statistical aggregates of alleles and haplotypes) and species; the organism (an entity present in Eldredge's reconstruction of the MS) was neglected as a fact of nature, relegated as a mere vehicle for the transmission of genes, or as an epiphenomenon with no significance whatsoever to evolutionary thinking (see also Ingold 1990, 2004; Nicholson 2014). The consensual definition of 'evolution' as any change in allelic frequency over time was the epitome of the restricted outlook of that ontology. Wagner (2015) also argues that the intellectual milestone that expanded the ontology of evolutionary biology was the 1981 Dahlem Conference on Evolution and Development held in Berlin (an articulation of the vision built on the idea that development needed to be integrated into evolutionary explanations; e.g. Gould 1977; Riedl 1978; Alberch et al. 1979). Following this author, the conception of the organism was 'reinvented' for evolutionary biology with the ensuing recognition of its variational properties (i.e. developmental constraints, variational modularity, facilitated variation and evolvability) and several structural aspects of organismal phenotypes (e.g. homologues/homology; modules/modularity; novelties; canalization; gene regulatory networks), predominantly by incorporating concepts derived from evolutionary developmental biology (Evo-Devo *sensu* Müller 2007). Whether the organism was neglected or not from mainstream evolutionary biology by the leverage of the MS (Wagner's and Eldredge's accounts, respectively), a theme that by itself deserves more systematic treatments from historians of biology, it is undeniably present in the contemporary ontology of the field, and its importance for evolutionary explanations is enormous. An essential piece of information for the point we want to make in this subsection (hinting at another epistemic bridge between HTE and the EES) is that the variational properties of organisms (*sensu* Wagner) have been incorporated into the emerging conceptual framework of the EES (see Laland et al. 2015). The 'reinvented organism' should be considered as a crucial component of the backbone of the EES.

In contrast, from early on, the HTE regarded the organism as a crucial player in the evolutionary process, but for different reasons than the ones championed by the structuralist tradition in evolutionism of which we believe G. P. Wagner is an heir. In *Unfinished Synthesis*, Niles Eldredge (1985, p. 143) identified organisms as the only shared instance between the ecological and genealogical hierarchies: "Note that organisms are included in both lists, a circumstance that is at once somewhat problematical and yet perhaps the crucial link between the two hierarchies". Back then, this author argued that the significance of organisms in the evolutionary process relied on the expression of their genes and them being the locus of natural selection; moreover, for Eldredge, the organism is the nexus between the environment (matter-energy transfer and conversion) and information (reproduction). But, what is an organism for the contemporary version of the HTE? We think that this question has not been properly addressed by the proponents of the framework. A possible epistemic bridge between the EES and the HTE could be built if the 'reinvented' characterization of the organism present in the former would also be used to redefine or reformulate the concept in the latter theoretical framework. The HTE seems open to integrate insights from Evo-Devo (see Pievani 2016a), and the redefinition of the concept of 'organism' could be a good start. A good example of steps aimed in that direction is the recent work by Italian philosopher of science Silvia Caianiello (2016), which revisits the phenotypic hierarchy (also called "somatic hierarchy") of the HTE by integrating insights from developmental gene regulatory networks and Evo-Devo, Eco-Evo-Devo, genotype-phenotype maps, and "homology thinking", among other themes also discussed by the EES.

Niche Construction

Organisms are not just beacons of heritable information: they modify their environments through their metabolism, activities and choices with significant ecological and evolutionary consequences. Niche Construction Theory (NCT) explicitly construes environmental modification by organisms ("niche construction" *sensu stricto*), and its legacy across generations (dubbed "ecological inheritance"), to be important evolutionary processes (Odling-Smee et al. 2003, 2013). Under this perspective, organisms exert influence over their own evolution by affecting natural selection regimes: niche construction modifies and stabilizes environmental states in nonrandom ways, thereby imposing systematic biases on the selective pressures acting on themselves and other species (Laland et al. 2015, 2016).

NCT is a major explanatory component of the EES (see Laland et al. 2015) and we are not the first to suggest that niche construction could be explored under hierarchical frameworks (see Pievani 2016a). Therefore, we see the potential common employment of niche construction as one of the strongest epistemic bridges between the HTE and the EES. For the HTE, the importance of the ecological hierarchy and of associated processes (especially of macroecological dynamics) as drivers of evolution is immense (see Lieberman et al. 2007; Eldredge 2008; Miller 2008). Niche construction can have profound effects on ecology, e.g. by affecting the distribution and abundance of organisms, changing the influence of keystone species, altering specific trophic relationships, and modulating the control of matter and energy transfer (Laland et al. 1999). Niche construction can also affect evolutionary rates, cause evolutionary time lags, upset responses to selection, and generate cyclical dynamics (Laland et al. 2016). Wider implications of niche construction for macroecology become apparent by the establishment of "engineering webs" in both communities and ecosystems, modifying, for instance, ecosystem resilience (Laland et al. 1999). Furthermore, niche construction can have causal interspecific influences in an ecosystem, leading to direct or diffuse coevolution, hence substantially changing the stability and dynamics of ecosystems on both micro- and macroevolutionary timescales (Laland et al. 2015). In summary, niche construction processes can outline several points of interaction between the genealogical and the ecological hierarchies not delineated previously by proponents of the HTE.

Pievani (2016b) states that niche construction is a good example of 'water sloshing in the bucket' (in reference to Eldredge's 2003 model) of the twin hierarchies: "Selective pressures come from the ecological hierarchy, affecting populations of organisms in their differential survival. But organisms can actively transform their environments for adaptive reasons and so construct new ecological niches that will be the frame of selective pressures for the next generations" (Pievani 2016b, p. 35). In addition, he proposes that these feedbacks and recursive processes occur at different levels and that such "multilevel niche construction" demonstrates the recursive relationships between the ecological and genealogical hierarchies (Pievani 2016b). We contend that this is one of the areas in which further collaborative work between advocates of NCT/EES and HTE might put our suggestion of epistemic bridges to the test.

Conceptual Rifts and Tensions Between the HTE and the EES: Multilevel Selection, Macroevolution, Ecological Inheritance, and Externalism

The Ambiguous Relationship of the EES to Multilevel Selection and Macroevolution (an Apparent Rift that Might be a Bridge?)

The Hierarchy Theory of Evolution consents and encourages the incorporation of the now well-studied phenomenon of multilevel selection (Pievani and Serrelli 2013; Pievani and Parravicini 2016; see Okasha 2006 for an overview). In the same sense, the study of macroevolutionary processes and patterns is a major concern for HTE research (Lieberman et al. 2007; Eldredge 2008), and one of the main reasons it was proposed in the first place: to attempt a successful explanation of macroevolutionary patterns, something the MS failed to do (Eldredge 1985; see also Lieberman 2016). Some advocates of the EES endorse multilevel selection in their individual publications (e.g. Pigliucci 2009; Sloan-Wilson 2010; Müller 2014), but that notion is apparently undervalued and scarcely mentioned in the most recent multi-authored portrayal of the structure of the EES (see Laland et al. 2015). Likewise, the current structure of the EES (Laland et al. 2015) lacks an explicit theory of macroevolution. Besides claiming that macroevolution is not 'microevolution writ large', and that evolutionary processes emphasized by this theoretical framework (such as developmental bias and ecological inheritance) help explain macroevolutionary patterns and contribute to evolvability, not much is said in that regard (see Laland et al. 2015). Two reasons could be alluded to explain these absences: on the one hand, future formal developments are simply needed; on the other, perhaps, the conceptual treatment of the extended ontology of evolutionary processes of the EES underestimates the importance of multilevel selection and/or of having a differentiated theoretical framework to robustly explain macroevolution. If the first option is preferred, an epistemic bridge between the EES and the HTE is in sight; however, if one complies with the second insight, this could represent a conceptual rift that might complicate the unification. As the EES allows for top-down causation, an important component in the literature of the levels of selection (see Okasha 2011), and expanded models of causation (see Sect. 2.2), the integration of multilevel selection into the working framework of the EES might not be onerous (although some authors could claim that this has already been done). In contrast, the articulation and integration of explanations of specific macroevolutionary patterns might prove to be more challenging for the EES. Four of such patterns (which are important for paleontologists defending the HTE stance; e.g. Lieberman et al. 2007) have not been addressed in the purported structure of the EES (Laland et al. 2015): these are geographic isolation, stasis, cross-genealogical turnover events, and mass-extinctions.

Paleontologist William Miller (2016, p. 245) recently summarized some of the critiques that emerged in the last decades from his camp toward the microevolutionary purview of the MS: "Empirical evidence from studies of (…) properties of species-lineages, speciation patterns (…), trends in clade history and differences in evolutionary rates, the possibility of species selection, and regional and global mass extinctions (…) indicates clearly that there is more to evolution than patterns resulting from scaled-up, gradual changes within demes". We think the same critique could apply to the evolutionary causes and processes studied by the EES: even though they might be of crucial importance, there is indeed still much more to evolution. The full gamut of (macro)evolutionary processes and patterns is not currently being addressed by that conceptual framework; in particular, many questions remain open regarding the *tempo* and *mode* of evolution (see Allmon 2016). In this context, we suggest that the EES should not turn its back to the evolutionary insights gained from paleontology and paleobiology. Without excluding other conceptual possibilities, a hierarchical view of nature (some may argue) could be the bridge to a theory of macroevolution that encompasses the extended ontology of evolutionary processes postulated by the EES.

HTE and the Challenge to Accommodate Ecological Inheritance and Other Extra-Genetic Channels of Heredity

NCT acknowledges two legacies that organisms inherit from their ancestors: genes and a modified environment with its associated selection pressures shaped by preceding rounds of niche construction (i.e. ecological inheritance; EI) (Odling-Smee et al. 2003). The evolutionary legacy described by the concept of EI strongly affects evolutionary dynamics (Odling-Smee et al. 2013; Laland et al. 2016), and contributes to parent-offspring similarity through the (re)construction of developmental environments, something critical for the development of many multicellular organisms and the recurrence of traits across generations (Badyaev and Uller 2009). In recent times, EI has become central to broaden the deeply entrenched and restricted conception of heredity held by the MS and the SET, as part of an inclusive view of inheritance that goes beyond transmission genetics and entails important evolutionary consequences (Danchin et al. 2011; Laland et al. 2016). The notion of 'inclusive inheritance' is paramount in extended frameworks of evolutionary theory (see Danchin et al. 2011), chiefly in the EES (see Laland et al. 2015).

It has been convincingly argued that EI differs in several features from genetic inheritance (Odling-Smee 2009; Odling-Smee and Laland 2011). First, EI is transmitted by organisms through the modification of the environment and not by "reproduction", and is not reliant on "ecological replication" or on the action of any sort of discrete replicators, as it depends entirely on sustained rounds of niche construction. In contrast to the biparental transmission of genes in sexual populations that happens only once for every reproductive event, EI "(…) is continuously transmitted by multiple organisms to multiple other organisms, within and between generations, throughout the lifetimes of organisms" (Odling-Smee and Laland 2011, p. 223). Additionally, genetic relatedness is not a precondition for EI, as it can be transmitted by other organisms (related through ecological interactions) in shared ecosystems.

As we will see, the unique characteristics of this legacy complicate the accommodation and interpretation of this notion under the HTE; in fact, we think that ecological inheritance subtends a profound conceptual rift between the EES and the HTE. The genealogical hierarchy, concerned with the conservation and transmission of information through reproduction or replication, involves genetically-based systems: the micro-evolutionary level of genes is nested within the upper level of organisms, which are components of local demes and so on, all the way up to monophyletic taxa of higher taxonomic rank (Eldredge 1985, 2008; Parravicini and Pievani 2016). The ecological hierarchy, on the other hand, is all about 'economic interactions', i.e. those that grant physical survival and involve matter-energy transfer (Eldredge 1986; see also Miller 2008; Cooper et al. 2016). Organisms are nested within local conspecific populations (namely, avatars), which are parts of local ecosystems that belong to regional ecosystems, up to the whole biosphere (Eldredge 2008; Pievani 2016a; Parravicini and Pievani 2016). If ecological inheritance does not implicate reproduction nor replication, and instead requires different processes from those involved in the transmission of genetic information, where exactly does it fit in the two interrelated, yet separate, hierarchies of the HTE? Is it confounded somewhere in the genealogical hierarchy, or is it more closely aligned to the intricacies of the ecological hierarchy? Furthermore, are the two hierarchies at all times and at all scales "non-coincident" (as claimed in Pievani and Serrelli 2013, p. 396)? This conceptual rift must be surmounted if the HTE and the EES are going to engage in a conversation regarding ecological inheritance.

Niles Eldredge, with a long-standing interest in the parallels between biological and cultural evolution of artifacts that led him to recognize the idiosyncrasies of the latter (see Eldredge 2000; Tëmkin and Eldredge 2007), has confronted similar issues in his attempts to use the HTE framework to tackle questions related to material cultural evolution (especially of complex systems such as human manufacturing of products, e.g. musical instruments, designed and built for the marketplace). His answer (Eldredge 2009) to the peculiarities of material cultural evolution relies on expanding the roster of hierarchies by inserting a third hierarchy between the two canonical hierarchies of "pure" information and economics.[3] This new hierarchy (that, in itself, is actually a dual structure of information and economics) refers to the actual 'makers' of material culture. So, the proposal of an additional hierarchy that specifically accommodates the intricacies of ecological inheritance and niche-constructing activities of organisms might function as a way out of the EI conundrum. Whether this turns out to be an *ad hoc* strategy only or a well-thought and sophisticated model, will be up to defenders of the HTE.

Similar problems for the HTE (but not as dramatic as the case of EI) emerge when we bring into the picture different channels of extra-genetic inheritance endorsed in the EES (see Laland et al. 2015): what to make of epigenetic and symbolic inheritance? (see also Jablonka and Lamb 2014). Where do they fit in the so-called "ontologically real" hierarchies of nature espoused by the HTE? For instance, epigenetic inheritance in the broad sense encompasses any inherited developmental variations that do not stem from differences in DNA sequence (e.g. cellular inheritance of self-sustaining feedback loops; structural inheritance of pre-existing membranes or cellular structures; chromatin markings such as covalent modifications in histones or differential methylation of nucleotides; RNA-mediated inheritance) or persistent inducing signals in the present environment (Jablonka and Lamb 2008). This view of epigenetic inheritance countenances soma-to-soma information transfers that bypass the germline (e.g. routes of transmission involved in the acquisition of symbionts and parasites; transmissions of developmental products from parents to offspring). Following Griesemer's notion of 'reproducer' (see Griesemer 2000, 2002), Jablonka and Lamb (2007, 2014) have argued that some epigenetic inheritance systems are reproducers without being 'replicators' (like genes supposedly are). A reproducer is a unit of multiplication, hereditary variation and developmental capacities, hence there is not exclusively an informational link but also material overlap between generations of reproducers (Szathmáry 2006). This is one example of the peculiar characteristics of epigenetic inheritance systems, among others, that hinders the idea of a genealogical hierarchy, as defended by the HTE, based on inter-generational transmission of information ensconced within genomes (but see Caianiello 2016).

Contrasting Stances on the 'Externalism-Internalism Debate'

The opposition between "internalist" and "externalist" viewpoints has been addressed in many historiographies of biology, psychology, philosophy and the social sciences (Godfrey-Smith 1996). Two illustrative examples of large-scale externalist programs are *empiricism* in epistemology (i.e. the philosophical stance that proclaims that the contents of thought are determined, directed or strongly constrained by the properties of experience) and *adaptationism* in biology. Seeing with adaptationist glasses is to understand biological structures, and evolution in general, as adaptive responses to environmental conditions; as recalled by Godfrey-Smith (1996, p. 32), "(t)he primary mechanism for this adaptive response recognized today is natural selection on genetic variants; genes are a channel through which the environment speaks". In contrast, biologists that uphold internalism usually assert that it is impossible to explain organic form, and the course of evolution for that matter, by simply attending to the structure or dynamics of the environments inhabited by organisms, where the latter thrive and reproduce. Furthermore, an internalist would say that "organic structure is strongly constrained, and in some cases determined, by internal factors associated with the integrated nature of living systems" (Godfrey-Smith 1996, p. 37). Independently, the historian and philosopher of biology Ron Amundson (2001) has suggested that the dichotomy characterized here as 'externalism-internalism' is just a revamped version of one of the oldest issues in comparative biology: the contraposition between "functionalist" and "structuralist" approaches with a common goal, which is explaining "organic form" (see also Sansom 2009). According to philosopher of science Denis Walsh (2015, p. 183), such dialectic opposition of explanatory views "has left an indelible mark on the history of evolutionary biology", and is pretty much alive today: "Many of the debates in current evolutionary biology and its philosophy take the form of a turf war, an attempt to carve out a larger territory for either the "internalist" explanations that advert to the inner processes of inheritance and development, or the "externalist" explanations that advert to the selecting influence of the environment" (*ibidem*). To finish this subsection, we point out an additional conceptual rift between the EES and the HTE: namely, the different standpoints held by these frameworks with respect to the 'externalism-internalism' debate.

Eldredge's (2003) Sloshing Bucket model, which is central to the HTE, is also relevant to the discussion between externalist and internalist viewpoints in the philosophy of contemporary evolutionary biology. Built by compiling evidence from geology, paleoecology and paleontology, his model of stability and change recognizes and exalts environmental change as the overarching

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[3] We should clarify that, for Eldredge, these hierarchies are only analogous to the biological hierarchies, with no ontological equivalency.

control of the evolutionary process. According to this model, in the history of life we see clear connections between the severity and scope of environmental perturbations and ecological disturbances, and the magnitudes of resultant evolutionary changes and effects (Lieberman et al. 2007; Pievani and Serrelli 2013). An example of those connections is the abiotic control of the evolutionary dynamics of stasis (see Eldredge et al. 2005). Eldredge (2008) posits that environmental jolts have matching evolutionary reactions (i.e. the bigger they get, the larger is the response), as water sloshing in a bucket. It seems that the proponents of the HTE align with an externalist view of evolution, but one fairly distinct from adaptationism. Here is an evocative excerpt of the externalist standpoint defended by the proponents of the HTE: "(…) the ultimate causal controls in evolution emanate, not from the genome, nor from environmental components of natural selection, but rather from the internal dynamics of ecosystems when critical points are reached through external physical environmental factors" (Lieberman et al. 2007, pp. 28–29). On the contrary, the EES is especially opposed to the kind of externalism instantiated by stringent adaptationism. In Pigliucci and Müller (2010b, p. 14) we read that "(t)he overcoming of gradualism, *externalism*, and gene centrism are general hallmarks of the Extended Synthesis" (emphasis added). Moreover, we interpret the global standpoint of the EES, albeit not explicitly stated in Laland et al. (2015), as a denunciation of the artificialness of the distinction between "internal" and "external" causal factors in development and evolution, and as a denial of the usefulness of maintaining the dichotomy for explaining organismal evolution. The proposal of reciprocal causation, in turn crucial for the EES, invites researchers to rethink the very same ideas of 'internalism' and 'externalism'.

If one posture fosters the dichotomy (strongly supporting one side) and the other encourages its abandonment, how to bridge the gap between these two radical explanatory views? After centuries of heated debates, is the EES on a right track by dint of dissolving the 'false dichotomy'? Can the primacy of environmental dynamics recede in future versions of the HTE, without distorting the core message of that framework? Notwithstanding the tensions implicit in this issue, we think that interesting empirical questions can be asked for the EES regarding important processes highlighted by the HTE (see Lieberman et al. 2007). For example, what happens with evolutionary processes such as niche construction, phenotypic plasticity, or genetic accommodation during the reorganization of a regional ecosystem or in the midst of a turnover pulse?

Final Remarks

This paper was written in the interest of encouraging scientific, philosophical and historiographical discussions about epistemological pluralism and/or theoretical unification in contemporary evolutionary biology, strictly focusing on commonalities and differences between the HTE and the EES. In this regard, some final points should be kept in mind for future discussions: What if the denunciation of the artificialness of the internalism–externalism dichotomy is the outcome of the organism-centered view of evolution defended by the proponents of the EES? As a matter of fact, Pievani points in this direction (2016b, p. 358): "While the views of the opposing side (the so-called standard theory) are polemically branded as "gene-centered" and too narrow (Laland et al. 2014), it is interesting to note that so far, the extended synthesis is strongly focused on organism as the fulcrum of evolutionary change". Pievani (2016b) also sees the 'organism-centrism' of the EES as a shortcoming and still as a restricted outlook, because evolution is a process occurring at different levels; in contrast, he claims that the "(…) hierarchy theory is a *different extended synthesis* able to cover all the levels that make the evolutionary game so complex, from genes to organisms to species and the largest ecological scenarios" (p. 360; emphasis added). Although we agree with this philosopher of biology that the organism-centered view of the EES (explicitly embraced by its proponents, see Table 1 of Laland et al. 2015) might have some drawbacks, we think that the reconstitution of the organism as an explanatory category for evolutionary biology, after it was concealed to the background by the MS and the SET, could prove to be a momentous triumph (see Bateson 2005; Pepper and Herron 2008; Nicholson 2014; Sultan 2015; Walsh 2015). Further reflections are needed to ponder and assess the consequences of a possible revival of organicism in biology (Gilbert and Sarkar 2000; Etxeberria and Umerez 2006; Denton et al. 2013; Nicholson 2014).

Practicing scientists, especially those interested in the long-dead biota, have recognized that in the study of organismal evolution there is an "epistemological gap" between the timescales and approaches used by neontologists when compared to paleontologists (Kemp 1999; Van Bocxlaer and Hunt 2013). In the same line of thought, some philosophers of science have argued that there is a genuine difficulty in combining the distinctive data of these two fields of scientific inquiry (Grantham 2004). Paleontologists face serious underdetermination problems when they try to excavate the underlying causal processes of the large-scale trends found in the fossil record (Turner 2009). On the other hand, paleontologists have disputed that "to extrapolate from ecological observations to events seen in the fossil record that took tens and hundreds of thousands of years to come to fruition requires a huge act of faith on the part of neontologists"

(Kemp 1989, p. 93). In fact, these two groups are traditionally, and notoriously, unfamiliar with each other's data, methodologies, epistemic assumptions, etcetera. That most of the proponents from the academic camps of the EES and the HTE are engaged, respectively, in the scientific and philosophical study of neontological phenomena (e.g. development; inheritance; niche construction) with an emphasis on *processes*, and paleontological issues (e.g. stasis; evolutionary trends; extinction; higher taxa) with an emphasis on *patterns* and *entities*, remains a major epistemological stumbling block to keep in mind for future discussions.[4] Possible avenues of cooperation may be pursed in the spirit of Elizabeth Vrba's (1993) assessment of how particular (ecological) processes may relate to patterns in the fossil record, where she famously reviewed a number of hypotheses that predict patterns of speciation and extinction (i.e. turn-over pulses, Van Valen's Red Queen, Red Queen steady state and stationary models), in an endeavor to tell apart the initiating causes of macroevolution that are physical from those that are biotic (this is a good example in which processes do not have to be treated completely disentangled from patterns; see also Vrba 1985, 2005).

Prospectively, additional epistemic bridges and conceptual rifts between the HTE and the EES might be suggested. Nevertheless, we also admit that it remains a challenge, to the proponents of both frameworks or for others scholars, to determine if the ones presented here are meaningful. In conclusion, one last question could be formulated: Are these epistemic bridges and opportunities for integration sufficient to overcome the conceptual rifts and explanatory tensions between the EES and the HTE?

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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[4] This aspect of the comparison between the HTE and the EES was pointed out by an anonymous reviewer.

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