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ARTICLE

Hierarchies, Networks, and Causality: The Applied Evolutionary Epistemological Approach

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Abstract

Applied Evolutionary Epistemology is a scientific-philosophical theory that defines evolution as the set of phenomena whereby units evolve at levels of ontological hierarchies by mechanisms and processes. This theory also provides a methodology to study evolution, namely, studying evolution involves identifying the units that evolve, the levels at which they evolve, and the mechanisms and processes whereby they evolve. Identifying units and levels of evolution in turn requires the development of ontological hierarchy theories, and examining mechanisms and processes necessitates theorizing about causality. Together, hierarchy and causality theories explain how biorealities form and diversify with time. This paper analyzes how Applied EE redefines both hierarchy and causality theories in the light of the recent explosion of network approaches to causal reasoning associated with studies on reticulate and macroevolution. Causality theories have often been framed from within a rigid, ladder-like hierarchy theory where the rungs of the ladder represent the different levels, and the elements on the rungs represent the evolving units. Causality then is either defined reductionistically as an upward movement along the strands of a singular hierarchy, or holistically as a downward movement along that same hierarchy. Upward causation theories thereby analyze causal processes in time, i.e. over the course of natural history or phylogenetically, as Darwin and the founders of the Modern Synthesis intended. Downward causation theories analyze causal processes in space, ontogenetically or ecologically, as the current eco-evo-devo schools are evidencing. This work demonstrates how macroevolution and reticulate evolution theories add to the complexity by examining reticulate causal processes in space–time, and the interactional hierarchies that such studies bring forth introduce a new form of causation that is here called reticulate causation. Reticulate causation occurs between units and levels belonging to *different* as well as to the same ontological hierarchies. This article concludes that beyond recognizing the existence of multiple units, levels, and mechanisms or processes of evolution, also the existence of multiple kinds of evolutionary causation as well as the existence of multiple evolutionary hierarchies needs to be acknowledged. This furthermore implies that evolution is a pluralistic process divisible into different kinds.

Keywords Applied evolutionary epistemology · Hierarchy theory · Networks · Upward causation · Downward causation · Reticulate causation · Time · Space · Spacetime · Pluralism

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1 Introduction and Outline

Applied EE understands and studies evolution as that what occurs when units evolve at levels of ontological hierarchies by mechanisms. Mechanisms define the means or conditions whereby change occurs, and these conditions in turn refer to processes.

Section 2 of this work briefly reviews how this general definition of evolution builds upon traditional adaptationist and non-adaptationist evolutionary epistemological approaches that study how evolution by means of natural selection occurs, and how a generalized selection theory can be applied to study knowledge processes. The elements that make up the general definition of evolution are briefly defined, and it is shown how Applied EE brings forth a methodology whereby evolving units, levels, mechanisms and processes can be identified, analyzed, and assessed.

Section 3 examines how, through this definition and methodology, Applied EE sheds new light on hierarchy and causality theories. Within the evolution of science in general and the evolutionary sciences in particular, causality theories are often cast in hierarchical terms. Causality theories are thereby formulated from within a rigid ladder-like hierarchy where causality is either defined as an up- or a downward movement along the strands of a single hierarchy. It will be shown that upward causation theories ally with reductionist explanations that understand causal processes in time, i.e. phylogenetically, over the course of natural history, as Darwin and the founders of the Modern Synthesis intended. Downward causation theories affiliate with holistic explanations that analyze causal processes in space, ontogenetically or ecologically, as proposed by the current eco-evo-devo schools.

Section 4 shows that macroevolutionary and especially reticulate evolutionary mechanisms and processes provide evidence that in addition to upward and downward causation, reticulate causation can be distinguished between units and levels belonging to the same as well as to different and interacting ontological hierarchies. Such causal processes are cast in both space and time, or space–time.

Section 5 concludes that beyond recognizing the existence of multiple units, levels, and mechanisms or processes of evolution, also the existence of multiple kinds of evolutionary causation as well as the existence of multiple evolutionary hierarchies need to be recognized. Evolution therefore is a pluralistic process divisible into different kinds.

2 Applied EE as a Theory and as a Method

Traditional adaptationist EE investigated how Darwinian selection theory can be generalized to explain how knowledge evolves, and knowledge was conceived broadly as including cognition, behavior, communication, language, and culture. Non-adaptationist EE in addition recognized the important role played by constructivist mechanisms and processes in bringing about the evolution of these phenomena, and in so doing, they helped to found the Eco-Evo-Devo approach.

Applied EE expands upon both traditional adaptationist and non-adaptationist EEs in the following way. Because evolution can proceed by a myriad of selectionist as well as non-selectionist evolutionary mechanisms and processes, Applied EE (Gontier 2010) provides a new and more neutral definition to evolution (Table 1), namely, *Evolution occurs when units evolve (change) at levels of an ontological hierarchy by mechanisms or processes*. From this definition a general methodology is derived for studying the various kinds of

Table 1 Applied Evolutionary Epistemology

1. Evolutionary theory (the epistemology of evolution)
Evolution occurs universally when *units* evolve (change) at *levels* of an *ontological hierarchy* by *mechanisms or processes*
2. Evolutionary methodology (the evolution of epistemology)
Studying any kind of evolution universally involves a search for units, levels, and mechanisms or processes, and allocating these into ontological hierarchies

evolution that exist, namely, *The study of any kind of evolution involves a search for units, levels, and mechanisms or processes, and allocating these into ontological hierarchies*.

This definition provides a new means to research the epistemology of evolution, while the methodology enables new research on the evolution of epistemology. In what follows, and by building upon previous work (Gontier 2017), the different aspects of the theory and methodology are explained in more detail.

2.1 Applied EE's Theoretical Definition of Evolution

Scholars within EE have contributed to the universalization of natural selection theory toward the cognitive and the behavioral sciences and they have often done so while working alongside evolutionary biologists. The universalization of selection theory (Cziko 1995) has introduced debates over what the heuristic (Campbell 1960) or universal skeleton (Lewontin 1970) of natural selection is as well as what the units (Lewontin 1970) and levels (Brandon 1982) of selection are. Traditional Darwinian selection theory stated that organisms evolve by means of natural or sexual selection at the level of the abiotic or biotic environment (Darwin 1859). Neo-Darwinian theory has gone further by internalizing natural selection and by demonstrating that the organismal body is also a locus of selection (Bickhard 2002; Lewontin 2000), as is the genome, where genes can be units of selection (Williams 1966, Dawkins 1976). In addition to genes, Universal Darwinism (Dawkins 1983) has conjectured that also memes (Blackmore 1999) can evolve as replicators at multiple levels of the evolutionary hierarchy. And replicator theory (Dawkins 1976) has been complemented with interactor theory (Hull 1981).

Evolutionary theories that developed at the margins of the Modern Synthesis or outside of the Neodarwinian framework have also identified new units, levels, and mechanisms or processes of evolution. Biophysicists, for example, have emphasized the important role that physical mechanisms and processes play in biological evolution (Kauffmann 2019, Prigogine 1980). Drift theory nowadays has a genetic (Kimura 1983) as well as an ecological component (Hubbell 2001) and drift theory has also been generalized and applied to cultural phenomena (Koerper & Stickel 1980). Macroevolutionary theories have drawn attention to phenomena such as punctuated equilibria (Gould & Eldredge 1977), stasis (Eldredge et al. 2005), and evolutionary constraints (Gould 1977). Scholars active in evolutionary developmental systems theory have argued that developmental cycles can be units of selection (Griffiths & Gray 1994; Oyama 1985), and such evolving entities have been called reproducers (Griesemer 2000). In physiology (Noble 2011), scholars are pointing toward developmental noise and biological relativity. Epigeneticists (Hallgrímsson & Hall 2011), molecular geneticists, and biochemists (Shapiro 2019; 2011) are demonstrating the unconventional ways wherein gene-protein regulatory networks and gene mobility take shape. In symbiology, the symbiont (Portier 1918; Wallin 1927), holobiont (Margulis 1991), and hologenome (Rosenberg & Zilber-Rosenberg 2013) have been recognized as units of selection as well as units of evolution in their own right (Sapp 1994). And also the principles whereby symbiont formation occurs are generalizable and applicable to understand how cultural chimera form (Gontier 2007).

Both selection theory as well as other evolutionary theories have thus identified units, levels, and mechanisms or processes whereby change occurs, and such is far from trivial. Rather, it informs us on what evolution is and how it proceeds. Applied EE therefore takes the universalization process that was started by traditional evolutionary epistemologists in the context of selection theory one step further by redefining evolution as that what universally occurs when units evolve at levels of ontological hierarchies by mechanisms and processes.

In what follows these concepts are further explained and focus thereby lies on how Applied EE redefines causal mechanisms and ontological hierarchies. The reader is also pointed toward the consequences of accepting this view, namely, Applied EE recognizes that there exist different kinds of evolution.

2.2 Defining Units

Applied EE favors a pragmatic rather than a metaphysical approach to defining concepts. Instead of philosophizing about the nature of units by listing the essential or inherent properties a unit must have for it to be recognized as such, Applied EE avoids *intensional* definitions and favors *extensional* and *ostensive* definitions (Table 2). The former are denotative, the latter demonstrative. Extensionally, units refer to the entity that evolves and these can be found by asking the "what evolves" question. Examples of units of evolution are replicators such as genes or memes, interactors, reproducers, symbionts, etc. What evolves is thus differential, and not all units are similar in kind.

Applied EE also adds an ostensive requirement to the identification of units and it requires the specification of the level/s where and the mechanism/s whereby that unit evolves. The specification of these levels is both necessary and sufficient to define a certain x as a unit.

Life demonstrates *unit plurality*: it is made up of different evolving units and each of these can evolve at different levels and by different mechanisms. Instead of a priori defining what a unit of evolution should be, it is therefore more pragmatic to point out where in an ontological hierarchy such possible units evolve and how, by which mechanisms or processes they evolve. Identifying such levels and mechanisms demonstrates and justifies that x is a unit of evolution.

Table 2 Ostensive and extensional/denotative definitions of units

	Epistemic question	Extensional/denotative definition	Ostensive definition
Unit	*What*	*The entity that evolves*	X is a unit if one can minimally point out one level where x evolves, and one mechanism or process whereby x evolves

Table 3 Ostensive and extensional/denotative definitions of levels

	Epistemic question	Extensional/denotative definition	Ostensive definition
Level	*Where*	The *locus* where evolution occurs	X is a level if one can minimally point out one unit that evolves by minimally one mechanism or process at x

2.3 Defining Levels

Extensionally, levels refer to the locus or place where the evolution of units occurs (Table 3). Ideally, this place can be located in space. Most of the time, however, scholars have to make due with an epistemological framework that provides theories on how space is made up of different ontological layers that function as places where evolution occurs (e.g. x evolves at the level of "the environment", "culture", "the genome", "the brain", "species", …). These frameworks thus take on the form of *ontological hierarchy theories* that try to capture the different biorealities (Gontier & Bradie 2017) that exist, and a level then refers to a strand on these hypothesized hierarchies.

Ostensively, one can demonstrate that x is a level in a hypothesized ontological hierarchy or in a bioreality if one can minimally point out one unit that evolves by minimally one mechanism or process at x.

Life also demonstrates *level plurality*: units can evolve by mechanisms and processes at different levels of one or more ontological hierarchies. Applied EE therefore also recognizes *hierarchy pluralism*, because for one, there exist different "genomes", "environments", "brains", "cultures", "species", etc. and secondly, one can track how these entities evolve in a myriad of hypothesized ontological hierarchies.

2.4 Defining Mechanisms and Processes

Extensionally (Table 4), mechanisms and processes refer to the means or conditions whereby evolution occurs, and mechanisms therefore associate with the how-question that asks for a listing of these conditions. Each of these *conditions* in turn refer to a specific set of *processes*. The conditions whereby natural selection occurs, for example, can be captured either by Campbell's (1974a) blind-variation-selective-retention heuristic, or by Lewontin's (1970) reformulation of the Darwinian principles as differential variation, inheritance, and differential fitness. And symbiogenesis can be conceptualized as occurring universally under the conditions that new entities irreversibly evolve out of the horizontal merger of previously independently evolving entities (Dyson 1998). In all cases, the units that evolve according to these

Table 4 Ostensive and extensional/denotative definitions of mechanisms

	Epistemic question	Extensional/denotative definition	Ostensive definition
Mechanism/ process	*How*	The *means or conditions* whereby evolution occurs	X is a mechanism or process if one can minimally point out one unit that evolves at one level by means of x

conditions (genes, organisms, cultural artifacts, etc.), and the levels where they evolve (the genome, organism, culture, etc.) can vary, but the conditions for change remain the same and it is these that enable the identification of the mechanism.

And ostensively, one can demonstrate that x is a mechanism or process if one can minimally point out one unit that evolves at one level by means of x (i.e. the conditions whereby x occurs).

Life also demonstrates *mechanism and process plurality*: besides by means of natural selection, evolution proceeds by means of drift, reticulate evolutionary mechanisms, developmental and epigenetic processes, physical mechanisms, etc. and these mechanisms and processes often occur simultaneously. Applied EE therefore also recognizes *causal pluralism*.

2.5 Applied EE as a Method for Evolutionary Research

While previous generations of evolutionary epistemologists have tried to examine evolution in singulars, Applied EE recognizes the plural nature of evolution as well as the need to further examine just how many units, levels, mechanisms and processes exist and how they underlie ontological hierarchies and bioreality formation. To that end, and from the definition given to evolution, the following evolutionary methodology is derived (Gontier 2017; 2018a). The study of any kind of evolution involves a systematic search for the units, levels and mechanisms or processes of evolution, allocating these into ontological hierarchies, and examining how they causally underlie the formation of different biorealities. Accordingly, Applied EE introduces three heuristics that systematically help to identify, analyze, and assess units, levels, and mechanisms or processes of any kind (Table 5).

Following the ostensive definitions given to units, levels, and mechanisms or processes of evolution, the heuristics begin by asking to identify either one by pointing out its relation to the other elements. Units cannot be units unless they evolve at levels by mechanisms or processes. Levels cannot be levels unless they house evolving units, and mechanisms or processes cannot be either unless they operate on or by units at levels according to specific conditions.

If successful in pointing out all three aspects of the evolutionary phenomenon under study, the heuristics generate further questions on timing, interactions, overlap, and relevance of the elements under study. These are further discussed in Gontier (2010; 2017; 2018a).

Here we focus on the specific questions raised by the heuristics for phenomena identified either as levels or as mechanisms and processes of evolution. In accordance with the extensional definitions given, when an entity is identified as a level of evolution, the level-heuristic asks about the ontological status of the level. And when an entity is identified as a mechanism of evolution, the heuristic asks to identify the conditions or processes whereby such a mechanism occurs. The former pertains to hierarchy theories, the latter to causality theories, and these now form the focus of the remainder of this article.

Table 5 Flowchart of Applied EE's methodology for evolutionary research (based upon Gontier 2017; 2018a)

IS X A *UNIT* OF (A SPECIFIC KIND OF) EVOLUTION?

?	Try to prove that x is a unit of evolution (1 example suffices); Go to yes.		
YES	**Where?** Identify the **level/s** where x evolves	Not one level found? X is not a unit; Go to no.	
		One/multiple level/s? *(Justification)*	How, **by which mechanism/s and process/es** did x evolve? *(Justification)*
	Since when?	When did x first **originate** in time and **when did x become a unit of (this kind of) evolution**?	
	How does x **interact** with other units?	Is x divisible into one or more **sub-or super-units**? If so, are they also units in evolution?	
	Is x also a **level** and/or a **mechanism or process**?	? and yes: Go to the level and/or mechanism/process-heuristic.	
	How **relevant** is x?	Is x **sufficient and/or necessary** for evolution or for theories thereof?	
NO	If not a unit, is x a **level** and/or a **mechanism/ process**?	? or Yes: Go to the level and/or mechanism/process-heuristic.	
		No: Treat x as irrelevant to evolution until proven otherwise.	

IS X A *LEVEL* OF (A SPECIFIC KIND OF) EVOLUTION?

?	Try to prove that x is a level of evolution (1 example suffices); Go to yes.		
YES	**How many/what units** evolve at x?	No units are identified? X is not a level; Go to no.	
		One/multiple unit/s? *(Justification)*	By which/How many **evolutionary mechanisms or processes** did the unit evolve at x? *(Test)*
	What is the **ontological status** of x?	Is x an **abstract notion** that facilitates theory formation, or an **existing entity**?	
	Since **when**?	Locate the **origin** of x in time or indicate when it becomes necessary to invoke x as an abstract notion in evolution theories.	
	How does x **interact** with other levels?	Is x divisible into **sub-or super-levels**? If so, are they also levels in evolution?	
	Is x also a **unit** and/or a **mechanism/process**?	? and yes: Go to the unit and/or mechanism/process-heuristic.	
	How **relevant** is x?	Is x **sufficient and/or necessary** for evolution or for theories thereof?	
NO	If not a level, is x a **unit** and/or a **mechanism/ process**?	? or Yes: Go to the unit and/or mechanism/process-heuristic.	
		No: Treat x as irrelevant to evolution until proven otherwise.	

IS X AN *EVOLUTIONARY MECHANISM OR PROCESS* OF (A SPECIFIC KIND OF) EVOLUTION?

?	Try to prove that x is an evolutionary mechanism or process involved in evolution; Go to yes.		
YES	On how many **units** is x active?	Not one unit: X is not an evolutionary mechanism/process involved in evolution.	
		One/multiple unit/s. *(Justification)*	At how many **levels** is x active? *(Test)*
	How does x work?	What **conditions** need to be met for x to occur? *(Requires universal heuristics of the working order of the mechanism.)*	
	Since **when**?	Locate in time **when** these **conditions are met** regarding each unit and each level.	
	How does x **interact** with other mechanisms/processes?	Is x divisible into **sub-or super-mechanism/s or processes**? If so, are they also mechanisms or processes of evolution?	
	Is x also a **unit** and/or a **level**?	? and yes: Go to the unit and/or level-heuristic.	
	How **relevant** is x?	Is x **sufficient and/or necessary** for evolution or for theories thereof?	
NO	If not a mechanism/ process, is x a **unit** and/or **level**?	? or Yes: Go to the unit and/or level-heuristic.	
		No: Treat x as irrelevant to evolution until proven otherwise.	

3 Defining Hierarchy and Causality Theories

Applied EE favors a pragmatic approach to defining units, levels and mechanisms. Nonetheless, there does exist a more metaphysical part to both the theory and the methodology when it analyzes how units and levels *causally* bring forth evolution and how they form ontological *hierarchies*.

Hypotheses on the nature of the world are formulated in hierarchy theories. Hierarchy theories are mediated by the epistemological framework used, a framework that is informed by perception and cognition, worldviews and theories, and scientific instruments (Gontier 2018b). Modern hierarchy theories trace back to the works of Simon (1962), Pattee (1973), and Mayr (1982), and these scholars formulated their ideas on ontological hierarchies from within the sciences of systems theory (von Bertalanffy 1950), cybernetics (Wiener 1948), and information theory (Shannon 1948).

Within these traditions, understanding phenomena hierarchically means that they are understood as complex systems (wholes) that are made up of subsystems (parts). Simon (1962, 468), for example, defined a hierarchy as “a system that is composed of interrelated subsystems, each of the latter being, in turn, hierarchic in structure until we reach some lowest level of elementary subsystem”. By adopting a systems-approach, Simon (1962, 468) sought to reformulate the then common inorganic–organic-superorganic hierarchical divide that characterized ontology thinking in his time. He instead distinguished between complex systems of a “physical”, “biological”, “social”, or “symbolic” kind. Examples he gave include, for physical systems, elementary particles that form atoms, molecules, and macromolecules; for biological systems, cells that in an upward manner organize into tissues that organize into organs that organize into systems, and cells that in a downward manner partition into subsystems such as the nucleus, cell membrane, and mitochondria; and for symbolic systems, an example Simon (1962, 469–470) gave was a book that is made up of chapters that are divided into sections, in turn divided into paragraphs, in turn divided into sentences, clauses, phrases, and words.

Modern hierarchy theories thus associate with complexity research and complexity is analyzed on the basis of the compositionality of systems. Compositional systems are described to have some unitary form of *functional organization* (synchronically), and this organization is argued to be brought forth by *emergent* properties that are irreducible to the systemic parts or subsystems. The question therefore becomes: How do the subcomponents of systems interact in such a way that they actually *bring forth* these emergent functional properties in *time* (diachronically), and that then introduces questions on evolutionary *causation*.

Hierarchy and causality thinking thus go hand in hand within the history of science, and causality is cast in hierarchical terms. Causality is understood in terms of *feedback loops* of *information flow* between ladder-like hierarchical systems where rungs of the ladder represent the different systems or levels, and the elements on the rungs represent the subsystems or units of which the levels are made up. Discussion then arises on causal *directionality*, with *reductionism*, and herein inspired by physicalism, defending the idea that information flows from the bottom of a hierarchy to the top, and *holism* recognizing that information can also flow from the top of a hierarchy to the bottom.

3.1 Types of Hierarchies and Causalities

From within this background, Ernst Mayr (1982), in his *The growth of biological thought*, attempted to define both biological hierarchies as well as evolutionary causation. Mayr (1982, 64–66) distinguished between two hierarchies: “aggregational hierarchies” (which he called an “arrangement by convenience”) and “constitutive” hierarchies (a hierarchy where “the members of a lower level, let us say tissues, are combined into new units (organs) that have unitary functions and emergent properties”). In a constitutive hierarchy, biological systems are classified based upon empirical data on common descent or development, and such differs from artificial classification systems amongst which he included the

Linnaean system of classification. The latter he called a downward classification imposed by the taxonomist that follows logical divisions, e.g. having or not having a specific trait (Mayr 1982, 205–207). Such a classification is inclusive in so far as higher taxa contain the subdivisions, but it is not constitutive of a new whole with new properties. It therefore remains an aggregation. A constitutive hierarchy instead is an inclusive hierarchy where units are thought to actually *bring forth* a new level "by a compositional procedure" (Mayr 1982, 207), and this new level has emergent properties not reducible to the independent parts. Aggregational and constitutive hierarchies, Mayr (1982) furthermore noted, differ from an exclusive hierarchy, where "a lower rank is not a subdivision of the higher rank". Examples he gave for the latter are scales of nature or military ranks.

Beyond Mayr's aggregational and constitutive hierarchies, ontological hierarchies have in the past also been understood as linear, and today, hierarchies are also becoming increasingly understood as interactional (Table 6).

How hierarchies have been conceptualized has thus been a cultural learning process, and the following part analyzes how aggregational, linear, nested, and interactional hierarchies bring forth different views on causality.

3.2 Aggregational Hierarchies and the Absence of Causality

An aggregational hierarchy refers to a *spatial* collection of units that are assumed not to interact in such a way that they constitute a new and functional entity. This redefines

Table 6 Hierarchical ways to conceptualize and visualize causality

Hierarchies	**Hypothesized Organizational Complexity**	**Visualizations**	**Causalities**
Aggregational	*Spatial* collection of units into an arrangement that lacks compositionality	Single set, one-level organizational chart, circle	**No causation** (descriptions)
Linear	Serial or sequential, successive or consecutive arrangement of units in *time*	Single line, trajectory, chain, scale, phases, stages, chronology	**Successive** (possibly discontinuous) or **consecutive** (continuous) **description/causation**
Nested (constitutive)	*Structural* arrangement of units into a new level; or the partitioning of a level into *functional* units	Multi-level organizational charts, bifurcating trees, Russian dolls, numerical timelines	**Up- and downward causation (**dual control) or **cyclic causation** (i.e. *recurring* up-and downward causation)
Interactional	Multidirectional, reticulate *interactions* between units belonging to different levels of the same or different hierarchies	Networks	**Reticulate causation**

Based upon and expanded from Gontier (2017)

Mayr's conceptualization of an aggregational hierarchy as an artificial one, because such clustering can happen either epistemologically (in theory) or ontologically (in nature).

Ontologically, a sofa, for example, can be arranged such that it contains two books, but these entities do not constitute the sofa, that one is made up of wood and fabric. The arrangement is man-made, as is the sofa, but the composition nonetheless happens in nature or better yet, in an evolved sociocultural niche.

Epistemologically, we can *describe* that spatial arrangement by clustering our notions of these entities into a set (of items on the sofa), or we can visualize them as a one-level organizational chart, or as a Venn diagram (also see Bechtel 2011 on visualizations). In all cases, the aggregational hierarchy has spatial locality and thus temporal existence, either in the niche, in the theory, or in the diagram.

But epistemologically, aggregational hierarchies do not hold assumptions on the existence of *causal* relations amongst the units that make up the hierarchy. Instead, from within aggregational hierarchies, the primary goal is to describe phenomena as they are in *space* (ontologically), and the elements are epistemologically classified into hierarchies by the use of cognitive criteria. In the given example of the books that are on the sofa, this expresses a state of affairs, but it does not provide a causal explanation for why they form this set.

3.3 Linear Hierarchies and Successive or Consecutive Causality

Hierarchies can also form as a result of units arranging into a series or a sequence over *time* and the hierarchy then takes on the form of a successive (possibly discontinuous) or consecutive (continuous) trajectory (Gontier 2018a). Examples of such linear hierarchies in ontology are polymerization reactions (monomers forming into polymers). And in epistemology, examples include chronologies or hypothesized time scales such as the geological, archaeological, or developmental time scales that respectively aim to depict or describe geological strata, archaeological finds, or developmental stages as seen by an observer.

The latter is important, because most linear hierarchies are organized cognitive sets that follow the flow of consciousness and the flow of hypothesized linear time. Following what Mayr (1982, 205–207) said on scales of nature and command hierarchies, these hierarchies are often exclusive: levels do not include the previous units of the hierarchy. The Upper Paleolithic, for example, is said to *follow* the Middle Paleolithic in time, but it neither includes it nor is it constituted by it. Another example are command hierarchies as we find them in military rank or in neural impulses. These also *appear* to follow a certain form of linearity, but their status as being successive or consecutive is unclear. The command or signal itself appears to be given continuously, but it takes on different forms over the trajectory it runs through, and the signal is discontinuous in so far as different entities are involved in the receiving, processing, and sending of it.

The epistemic use of conceptualized linear hierarchies marks the beginning of historical time thinking or natural history research that saw the rise of fields such as history, chemistry, anthropology, and linguistics. These disciplines understood the chronology of events as single trajectories. But understanding events as the outcome of a single trajectory often leads to false causal reasoning. That in most places humans follow Neanderthals in the geological strata, for example, gives an accurate empirical *description* of the fossil record, but humans did not *causally* evolve from Neanderthals. Rather, Neanderthals are our cousins with whom we interbred and with whom we share common ancestors. One can thus wonder whether linear hierarchies are at all adequate to describe compositional aspects of reality. Mayr instead called hypothesized stages and scales artificial classification systems and he distinguished these from natural ones. Nonetheless, these stages and classification systems are real in so far as they coincide with existing theories that were once thought to be real in the eyes of their beholders.

3.4 Nested Hierarchies and Up–Downward, or Cyclic Causation

Most of the hierarchies that scholars study, including those that plead for an Extended Evolutionary Synthesis (Pigliucci & Müller 2010), are nested hierarchies (Grene 1987). These hierarchies were introduced into evolutionary biology by Mayr (1982, 65) who in the process called Simon's (1962, 468) hierarchies "constitutive" hierarchies. And following Pattee (1973), Mayr combined system thinking with thinking on emergence by noting that "[i]n such a hierarchy the members of a lower level, let us say tissues, are combined into new units (organs) that have unitary functions and emergent properties." In Mayr's constitutive hierarchies, the interacting units at one level thus not merely compose into a new level. The units are thought to actually bring forth or *cause* the new level. And the new level is assumed to form a new whole that demonstrates emergent properties that are irreducible to the lower units wherefrom it is constituted.

Examples, for Mayr (1982, 64), include a developmental hierarchy that goes from cells to tissues, organs, and functional systems; and an "evolutionary" (Hull 1980; 1981) hierarchy where genes arrange into organisms that arrange into species based upon common descent. When Hull (1980) defined the evolutionary hierarchy, he not only built upon Mayr's work, he also invoked this hierarchy with the goal to integrate important insights coming in from micro-meso- and macroevolutionary studies. For Hull, the genes-organisms-species hierarchy is based upon the genotype–phenotype distinction (Pattee 1973) or what Dawkins (1976) later called the replicator-vehicle distinction. Examples of replicators are genotypes or genes. Examples of vehicles are phenotypes but also chromosomes, cells, organisms, species, communities, and ecosystems. Dawkins (1976) went on to develop a gene-reductionist point of view that emphasizes the importance of replicators over vehicles. And Hull (1980) countered these ideas by emphasizing holistic views that recognize the evolutionary importance of vehicles in ecology and development, for which he introduced the notion of interactors.

Evolutionary hierarchy thinking furthermore underlies theorizing on upward and downward causation (Table 7). Upward causation (Craver & Bechtel 2007; Rosenberg 2020) is defined as the process where units residing at "lower" levels bring forth "higher" levels. Genes, for example, bring forth organisms that group into species. Downward causation (Campbell 1974b, 182; 1990; Emmeche et al. 2000; Paoletti & Orilia 2017) is defined as the process where units residing at "higher" levels in a hierarchy impact units residing at "lower" levels. During ontogeny, for example, functional systems are said to impact organogenesis and cell differentiation.

Note that upward causation is studied as a process over *time*, and as such it associates with the rise of natural history research that gave way to the field of evolutionary biology as we know it. Downward causation, although sometimes understood in timely terms as a form of backward or retro-causation, is mostly studied as a process that occurs in *space*. Here, it finds its applications in fields such as ecology that studies organisms in the economy of nature, and ontogeny that studies the developmental life course of the organism. Upward causation theories moreover focus on *affordances* or evolutionary potential, and downward causation theories emphasize the existence of

Table 7 Affordances and constraints resulting from up- and downward causation

Causality	Research fields	Evolutionary outlook	Research focus
Upward causation 	Natural history Phylogeny (genetics)	Affordances	Temporal change
Downward causation 	Ecology Ontogeny (developmental biology)	Constraints	Spatial change

constraints imposed by development or ecology on that evolutionary potential (Futuyma 2010; Gould 1977; Schank & Wimsatt 1986; Wagner & Altenberg 1996).

Through downward causation, Polanyi (1968) noted, nested hierarchies have an element of *dual control* or dual directionality where, as noted by Grene (1987, 505), “the lower level units provide material for the arrangements at upper levels and the upper level arrangements constrain and thus control the activities of the lower levels”. An example is a biological organism that is built by genes, while that organism then controls or constrains the spread of the genes through reproduction. Craver and Bechtel (2007) have argued that dual control and downward causation can be understood as a form of upward causation recurring cyclically (Bechtel 2011).

And debating the existence of up- and downward causation also underlies debates on the units and levels of selection (Dawkins 1976; Gould & Eldredge 1988; Hull 1980; Okasha 2005; 2012; Stanley 1975; Vrba & Gould 1986), the nature of biological individuality (Ghiselin 1974), and theorizing about the major transitions of evolution (Maynard Smith & Szathmáry 1995) where scholars assume that besides emergent properties, critical thresholds need to be passed to enable the “leveling up” of a hierarchy.

3.5 Interactional Hierarchies and Reticulate Causation

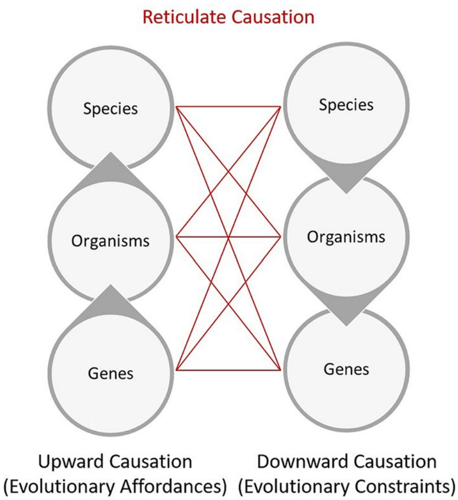
Dual or cyclic causality remains confined to causality going up- or down a singular hierarchy, or to doing so repeatedly. Eldredge (1985a, b; 1995) has gone one step further by combining the hierarchies proposed by Dawkins and Mayr/Hull into a double hierarchy. From the 1980s onward, Eldredge and coworkers (Eldredge & Salthe 1984; Vrba & Eldredge 1984; Eldredge 1985a; 1995) have separated "a genealogical or replicator-based hierarchy" from an "economic or interactor-based hierarchy". Within a genealogical hierarchy, life forms a nested hierarchy of common descent that is based upon organisms that transfer an informational genetic code thereby bringing forth demes, species, and clades. And following Ghiselin's (1974) notions of biological individuals and Hull's (1980; 1981) notion of interactors, in their non-replicative and non-reproductive aspects, organisms exchange matter and energy in a nested ecological hierarchy than runs from proteins and organisms all the way through to populations, communities, and ecosystems (Tëmkin & Eldredge 2015). Both of these hierarchies are also recognized to interact with one another, and visualizations thereof already bring forth network-like diagrams.

But network science (e.g. Watson et al. 2020) is currently flourishing largely in part to its ability to visualize reticulate evolutionary processes as they occur by symbiosis, symbiogenesis, lateral gene transfer and infective heredity (Gontier 2015). Networks differ from the classic, ladder-like hierarchies and instead depict *interactional hierarchies* (Gontier 2017) that are characterized by what we here call *reticulate causation* (Table 8). Reticulate causation occurs between units and levels belonging to *different* as well as to the same ontological hierarchies.

The difference is best illustrated by returning to Simon's original work on complex systems. For Simon (1962, 468, my italics), a hierarchy refers to "all complex systems analyzable into *successive sets* of subsystems," and the application of the term successive here implies an assumption on linearity in time. As noted earlier, examples he gave include eukaryotic cells that organize into tissues that organize into organs that organize into a biological system; and eukaryotic cells in turn are "well-defined subsystems" made up of a nucleus, cell membrane, and organelles.

Such is an excellent hierarchy if the primary goal is to explain how life evolved on earth during the course of natural history, or how individual eukaryotic cells are

Table 8 Reticulate causation



structurally composed of functional parts, but such constitutive hierarchies are not well-suited to explain ontogenetic or ecological interactions between different cells, or between the nucleus and organelles. Organelles, for example, can exchange genes horizontally with the nucleus of the cell they belong to (Doolittle 1999), and thereby alter the evolutionary trajectory of all parties involved. Or they can exchange genes with ontogenetically acquired viruses (Shapiro 2011) that were following a different evolutionary trajectory. During hybridization, organisms belonging to different families, orders and even classes reproduce and form new individuals. And during holobiont formation (Margulis 1998), reticulate causal relations between organisms from different kingdoms and domains of life result in the formation of spatiotemporally-bounded new biological individuals that simultaneously function as new habitable zones of life (Gontier 2018b).

Similarly, a developmental hierarchy is useful to describe how organisms develop from zygote to adult, and in that regard, a human body, for example, is indeed the sum of its tissues and organs. But once in existence, human anatomy is controlled by the intake and excretion of water and food in an ecological hierarchy (Tëmkin & Eldredge 2015) that is in turn undergoing sociocultural modifications. Neurologists moreover have demonstrated that much of the behavior displayed by the human body is controlled by the brain and the central nervous system. Functional behavior thus results from the interaction of units and levels that partake in *different* hierarchies.

Instead of merely identifying the units and levels that constitute hierarchies and depicting these trajectories into linear hierarchies, one can focus on the intra- and inter-level reticulate interactions between hierarchical entities, and visualize them into networks. And these networks remain hierarchical, simply because they lend insight into different focal points (of control or attraction, for example).

Today, developmental and ecological interactions in general, and the eco-evo-devo and reticulate theories that make sense of them in particular, have also demonstrated that interactions can be stronger between systems that within systems. And this again counters Simon (1962, 473) who argued that complex systems form more rapidly if there are intermediate and stable subsystems, and that interactions within a system (intra-level) are stronger than interactions between systems (inter-level).

Humans, for example, often only reproduce a couple of times (something that is studied from within the genealogical hierarchy), but during their lifetime, humans interact with their microbiome, viriome, and numerous other species in non-reproductive ways. An average male weighing 70 kg, for example, is built up of around 30 trillion cells, while he "carries" with him, during his life course, a variable microbiome made up of around 39 trillion bacteria (Sender et al. 2016). The different body parts in turn interact with that microbiome in symbiotic ways, and the microbiome contributes to health and disease, as well as cognition and behavior (Archie & Tung 2015).

The assumed causal directionality of linear (one-way) and dual (nested) hierarchies is therefore anything but straightforward. Instead, there can exist reticulate causal interactions *within* units and levels that constitute a particular hierarchy, and *between* different units and levels belonging to different hierarchies.

3.6 Summarizing the Part on Hierarchy and Causality Theories

Hierarchy theory originally focused on distinguishing the rungs or levels of a hierarchy, and only secondarily did it focus on the interactions between the units of those rungs, or the interactions between different rungs. Much of these interactions have been formulated from within theories on emergence, the systemic or functional nature of the components of the hierarchy, its naturalness, inclusiveness, embeddedness, or individuality. But many of these characterizations are not needed to identify hierarchies as nested. Ontologically, a wooden desk, for example, can be arranged such that it contains papers, a coffee cup, and a computer. These entities do not constitute the desk, that one is made up of wood, and the entities neither emerge from the desk nor are they inherently part of it. Nonetheless, the desk arranged in such a way composes into a *new* environment that can function as a temporal workspace. But most importantly, such happens if and only if a third party (e.g. an organism made up of tissues and organs, with a brain that gives commands to muscles), from *outside* the existing setup, recognizes the hierarchical arrangement as indeed a spatiotemporal workspace.

Here too, a *pluralistic* stance is thus needed. Hierarchies need to be conceptualized as multiple, and the challenge is to examine how many hierarchies can be distinguished, and how *reticulate causal interactions* occur between *distinct* hierarchical systems. For a long time, scholars have held polemic debates on which hierarchy is the most correct one, i.e. which hierarchy is the most in one-to-one correspondence with reality. But the fact of the matter is that all hierarchical types exist in nature, and these hierarchies in turn lend insight into the nature of different ongoing processes in space and time. Choosing which ontological hierarchy is applied epistemologically is therefore determined by the phenomena accounted for in the developing theories.

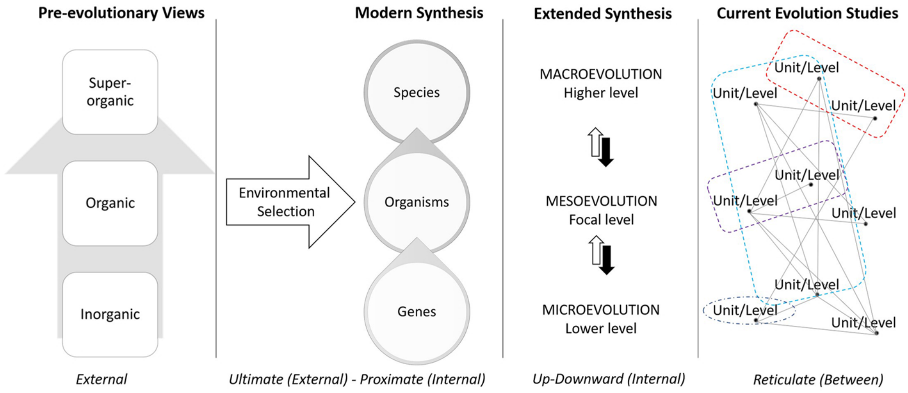
4 Causal Reasoning in the Light of Space, Time, and Space–Time

Recent years have seen a continued interest in explanatory (Braillard & Malaterre 2015), mechanistic (Glennan 2017; Rosenberg 2020), and causal thinking in general (Beebee 2015; Cartwright 2004; Godfrey Smith 2010; Illari & Williamson 2012), and in particular in how the concept of causation is applied in molecular and cell genetics (Bechtel 2019; 2020), evo-devo (Baedke 2020), cognitive psychology (Menzies 2012), medicine (Clarke et al. 2014), and the social sciences (Russo et al. 2019). Here, it was investigated how the evolutionary biological sciences have conceptualized causation from within hierarchy theories and this has brought to light the crucial role changing views on space and especially time play in the development of both hierarchy and causality theories.

Under 2.1, mechanisms were defined as the means or conditions whereby change occurs, and these conditions in turn refer to processes. Nonetheless, in the literature, mechanisms and processes have often been considered opposites (e.g. Dupré 2020). *Mechanisms* moreover have been argued to provide *explanations* while *processes* are said to provide *descriptions* (Rieppel & Grande 1994; Nuño de la Rosa and Etxeberria 2012; Gontier 2016). In this regard, and when discussing how the complexity of biological and cultural systems is handled by scientists, Simon (1962, 479) differentiated between "state" and "process" descriptions, and he gave the following examples:

> 'A circle is the locus of all points equidistant from a given point'. 'To construct a circle, rotate a compass with one arm fixed until the other arm has returned to its starting point'. It is implicit in Euclid that if you carry out the process specified in the second sentence, you will produce an object that satisfies the definition of the first. The first sentence is a state description of a circle, the second a process description. (Simon 1962, 479).

Table 9 Evolving views on the locus of causality in the evolutionary sciences



Simon (1962, 478) furthermore noted that "[t]he most common recording of descriptions of dynamic systems consists in replacing a description of the time path with a description of a differential law that generates the path" (Simon 1962, 478). The description of the trajectory over time is often replaced by a force or law that is said to bring forth the trajectory. Such however marks an older and pre-evolutionary way wherein causality has been conceptualized, one where laws are understood to be *external* to the path (Table 9).

This kind of reasoning also characterizes the founders of the Modern Synthesis who understood genes to bring forth organisms that bring forth species (an upward hierarchy), but natural selection remained understood as an *external environmental force* that acts upon organisms in such a way that the distribution of organismal genes across generations is differential.

When Mayr attempted to define causation, he therefore distinguished between *proximate* causes such as physiological causes that explain the functionality of the system *synchronically*, i.e. from *within* the system, and *ultimate* or *diachronic* (evolutionary) causes. Rather than locating the latter as coming from outside the hierarchy, Mayr wanted to synthesize proximate (synchronic) with ultimate (diachronic) causes because in his attempt to define a constitutive hierarchy epistemologically and synchronically, Mayr also tried through that definition to explain how new entities evolve ontologically and diachronically (Mayr 1961; Tinbergen 1963; discussed in Gontier 2012). Thus, through the definition of the state of the evolutionary hierarchy, he wanted to explain the process of how it evolved over time. Mayr's proximate causation is thus a form of upward causation and as such it can be defined *internally*, from within a single hierarchy, and reductionistically, by how genes function to bring forth the organisms and species. But Mayr's ultimate causation does not (yet) match with downward causation occurring within the same system or hierarchy. Rather, it refers to causes that are *external* to an existing system or hierarchy, because selection remains defined as that what occurs within the environment. Hence also Van Valen's (1973) research on ecology where he emphasized that the environment where selection occurs is not only abiotic, rather it is also made up of other organisms. Through his study of ecology, Van Valen's work can therefore also been seen as an attempt to bring the biotic environment *into* hierarchy thinking (either as a separate ecological hierarchy, or as an aspect of the genealogical hierarchy).

Evolutionary sciences today no longer think in terms of eternal "laws" or "forces" that act upon nature while they remain external to it. Rather, causality is nowadays defined from *within* hierarchies, through the internalization of selection, the inclusion of the ecological hierarchy, and the recognition of niche construction as an extension of biological evolution.

Focus thereby has laid on describing the paths. Bechtel and Richardson (1993), for example, and in that building upon Simon's distinction between state and process descriptions, define mechanisms as "systems that produce a phenomenon of interest by means of the organized and coordinated operations [the process aspect] performed by their parts [the state aspect]." As such, causality becomes part of the conceptualized hierarchy, and synchronic and diachronic research start to converge. Machamer et al. (2000, 3), and by building upon both Simon and Bechtel & Richardson, define mechanisms as "entities and activities organized such that they are productive of regular changes from start or set-up to finish or termination conditions." These definitions of mechanisms integrate both types of Simon's descriptions, and they furthermore take into account the fact that the parts of a level often already consist of units (or subsystems as they prefer).

Thus, with the rise of (post-)Neodarwinian thinking, causes become defined from *within* the hierarchy, as up-and downward causation. And such, however, brings forth problems on time. Craver and Bechtel (2007) pointed that out when they tried to understand downward causation as something that can be reduced to cyclic explanations of lower-level parts/entities and their operations/activities. And Bechtel (2011) has later used concepts such as feedforward and feed backward loops that, because these can be *recurring in time*, portray a cyclic causality.

I agree with Bechtel (2011), that a mere description of a sequential series of qualitatively characterized operations is not sufficient to capture the often cyclic organization found in biological systems. Cell regenerations that occur quite frequently throughout the human life course, or complex phenomena such as the Krebs cycle, show that neither the parts nor the dynamic operations thereof are static. Rather, these systems rejuvenate and self-maintain because of a constant uptake and excretion of matter and energy, where dual causality follows complex feedback loops. Describing these cyclic and thus recurring flows of matter and energy requires a dynamic understanding of mechanistic explanations, and these differ from classic, lineal descriptions of trajectories that go from A to B.

Nonetheless, I disagree with Craver and Bechtel (2007), that downward causation can be reduced to cyclic explanations of lower-level parts/entities and their operations/activities, because *thirdly*, during such cycles, phenomena need to be taken into account that lie *outside* of the spatial trajectory under analysis, and also the *time interval* of events become different (Table 10). And here, how these hierarchies interact with one another in network-like typologies needs investigation.

Today, there is a tendency to break free from the rigid linear or bidirectional way wherein causality has been understood, and scholars are more and more recognizing the reticulate nature of causal processes. And this brings forth new means to conceptualize ontological hierarchies and the causality that exists between them. Reticulate causation necessitates us to break free from existing hierarchy thinking, as focus shifts from one hierarchy that is made up of one kind of units and levels, to the interactions that exist between different units and levels belonging to different hierarchies. Not the units and the levels but the interactions

Table 10 Complementing state and process with reticulation

Ontological Aspect	Epistemic Outlook	Causal Explanation
State	Synchronic (in space)	Proximate causality
Process	Diachronic (in time)	Ultimate causality
Reticulation	Interactional (in spacetime)	Reticulate causality

between them define the hierarchies, and this enables one to break into research on bioreality formation.

Summarizing, hierarchies have been the means *par excellence* for how scholars conceptualize causality and this has been characterized, first by a tendency to *internalize* causality as something that occurs within the hypothesized system or hierarchy; secondly, by recognizing that there exist *multiple* hierarchies, and finally, by realizing that there exists *reticulate causality* between them. So beyond the current *spatial* state of a hierarchical system and the process whereby it came about in *time*, a valid research avenue is how that hierarchical system interacts reticulately with other hierarchies in *spacetime*.

The latter furthermore not only requires us to take the interactions of different hierarchies into account, it also requires us to acknowledge the different periodicities of the events. Scholars active in evo-devo schools and symbiogenesis have made us realize that evolution can occur at a much faster pace than predicted by natural selection. And recognizing that time can be differential based upon what kind of mass is under examination, in turn, is more in line with current advances made in quantum physics.

In other words, when studying interactions between a genealogical and ecological hierarchy, it becomes necessary to situate the linear hierarchy that has been plotted into a larger framework (multidimensional vector space), and to investigate how factors outside that specific hierarchy are necessarily part of the explanation of the focal level of interest. This move implies that causal explanations cannot only be linear, there exist factors that perturbate an otherwise linear sequence from the outside. And this brings forth the non-linear dynamics so typical of network hierarchies. But at present, the *differential time intervals* of the processes mapped remain understudied (but see Watson et al. 2020).

5 Epistemic Pluralism and the Recognition of Different Kinds of Evolution

Currently, advances made in fields excluded from both the Modern as well as the Extended Evolutionary Synthesis are bringing forth a scientific revolution in the evolutionary sciences. These new sciences have started to re-conceptualize the classic assumptions made in traditional hierarchies on causality, linearity, and compositionality or individuality in time. Much of this can be captured by looking into the new means wherein scholars map and model how parts of wholes not only form *multiple* hierarchies in space (ecology) or time (genealogy), but how they in turn interact *reticulately* in spacetime or what has been characterized as an extended present (Gontier 2018b), and these interactions nowadays often take on the form of network-diagrams.

The history of evolutionary science is filled with polemic debates on what the true units and levels of evolution are, which diagram is best able to capture how units and levels structure into a hierarchy, and which mechanisms are best able to explain the evolution of the units and levels, and how the levelling up or control in a hierarchy occurs. The above demonstrates that the time has come to recognize unit, level, mechanism, hierarchy, and causal pluralism.

From this follows that there exist different kinds of evolution, and that is the final tenet of Applied EE. Evolution by means of natural selection is different from how it occurs by means of eco-evo-devo or symbiogenesis, it often implies different units and levels, and these types of evolution can and have to be conceptualized from within more than one epistemological hierarchy, by mapping the interactions between them in network-like typologies.

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Conflicts of interest None.

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