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Evolutionary Epistemology: Two Research Avenues, Three Schools, and A Single and Shared Agenda

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Abstract

This special issue for the *Journal for General Philosophy of Science* is devoted to exploring the impact and many ramifications of current research in evolutionary epistemology. Evolutionary epistemology (EE) is an inter- and multidisciplinary area of research that can be divided into two ever-inclusive research avenues. One research avenue expands on the EEM program and investigates the epistemology of evolution. The other research avenue builds on the EET program and researches the evolution of epistemology. Since its conception, EE has developed three schools of thought: adaptationist, non-adaptationist, and applied EE. Although diverse in outlook and theoretical background, these research avenues and schools share the same agenda of understanding how knowledge evolves, and how it relates to the world. In this paper, we first explain wherefrom evolutionary epistemological schools of thought developed, and then we highlight current debates in EE by briefly reviewing the papers that form part of this special issue.

Keywords Evolutionary epistemology · EEM program · EET program · Adaptationist EE · Non-adaptationist EE · Applied EE

This special issue for the *Journal for General Philosophy of Science* is devoted to exploring the impact and many ramifications of current research in evolutionary epistemology. Evolutionary epistemology (EE) is an inter- and multidisciplinary area of research that can be divided into two research avenues and three schools that although diverse in outlook and theoretical background share the same agenda. Here, we place these traditions into historical perspective and then we move on to current debates raised by the authors that contribute to this special issue. We end by pointing toward directions for further research.

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1 Two Ever-Inclusive Research Avenues

Evolutionary epistemology took flight as an attempt to naturalize philosophical research by understanding the act of cognizing, and also the outcome of cognition, i.e. knowledge, as evolving phenomena. The evolution of knowledge comprises both the evolution of the biological substrate and mechanisms that underlie cognition and the capacity for acquiring and processing knowledge, on the one hand, and the evolution of knowledge as expressed in theories, practices and behavior, on the other. It is not obvious that processes that account for the evolution of the former are capable of explaining or illuminating the latter. Bradie (1986, 403) therefore divided EE into two research programs, EEM and EET. In the EEM program focus lay on the Evolution of Epistemological Mechanisms, and this implied research on how cognition evolved in humans and other animals. In the EET program, attention was given to the Evolutionary Epistemology of Theories, and this implied an investigation on the growth of scientific knowledge and how the evolution of scientific theories can be understood by analogy with biological evolution theories. Today, research on cognition has expanded toward a study of knowledgeable processes as they occur at a molecular, biological, sociocultural, and technological level. And the vast expansion of evolutionary theories within and outside of evolutionary biology has paved the way for a wider study of the nature of evolution and theorizing thereof.

EE today is concerned equally with the evolution of epistemology as with the epistemology of evolution (Table 1). In the former sense, EE investigates the evolutionary origin, change, and transmission of information, knowledge, and knowing in molecular systems, living organisms, and technological complexes and it therefore associates with the biochemical, anatomical, behavioral, cognitive, sociocultural, and technological evolutionary sciences. In the latter sense, EE investigates what and how one knows about evolution and here it associates with the fields of theoretical biology and (philosophy of) the evolutionary sciences that develop evolutionary theories and methodologies. Both research avenues make EE of continued relevance for scholars active in any and all of these fields, and the avenues also cross one another because how one knows about evolution is dependent upon the evolution of knowing subjects.

EE has significantly contributed to the advancement of the disciplines listed in Table 1 and it has also co-evolved with the progress made in these fields.

2 Three Schools With a Shared Agenda

There exist three distinguishable schools of evolutionary epistemological thought: traditional, non-adaptationist, and applied EE (Table 2). Here it is briefly reviewed how these schools contribute to both of EEs research avenues.

Table 1 EE's two research avenues expanded

EEM => The evolution of epistemology	EET => The epistemology of evolution
How information, knowledge, and knowing evolve	What (theories) and how (methodologies) one knows about evolution
Biochemical, anatomical, behavioral, cognitive, sociocultural, and technological evolutionary sciences	Theoretical biology & (philosophy of) the evolutionary sciences

Table 2 Differences between Traditional, Non-Adaptationist, and Applied EE

Aspect of difference	Traditional EE	Non-adaptationist EE	Applied EE
Evolution of Epistemology			
Evolutionary Framework	Strict-Neodarwinian	Systems Theory (Current Eco-Evo-Devo Schools)	Pluralistic (Neo-Darwinian, Eco-Evo-Devo, Reticulate Evolution, Drift Theories, …)
Organism-Environment Relationship	Dualistic, Adaptationist	Dialectic, Non-Adaptationist	Constructivist
Worldview	Hypothetical Realism	Coherence Theory & Cognitive Constructivism	Spatiotemporally-Bounded Realism
Epistemology of Evolution			
Evolutionary Hierarchy	Gene/Trait-Focussed	Organism-Focussed	Units, Levels, Mechanisms-Focussed
Causation	Upward	Up- and Downward	Reticulate
Explanation	Reductionist	Holistic	Integrative
Situatedness	In Time (Phylogeny)	In space (Ontogeny & Ecology)	In Space-Time (Multiple Biorealities)

Concerning the *evolution of epistemology*, the founders of what today can be called traditional evolutionary epistemology, such as Lorenz (1941; 1958), Campbell (1960; 1974a; 1997), and Popper (1963; 1972) contributed to the implementation of Neodarwinian evolution theory (Provine & Mayr 1980) into the ethological (Tinbergen 1963) and the behavioral sciences (Skinner 1981) as well as to the cognitive philosophical (Bradie 1986; Bradie & Harms 2020; Hull 1988; Munz 1993; Rorty 1980; Ruse 1986; Toulmin 1972; Vollmer 1975), and sociocultural sciences (Lumsden & Wilson 1981). By understanding natural selection as a global learning process, and by adhering to strict adaptationist views, these scholars developed hypothetical realist theories on knowledge and knowing. They understood evolved knowledge to corroborate to truth through blind trial and error processes (Popper 1963), and evolving organisms and their traits were understood to be adapted to the world through blind variation and selective retention (Campbell 1974a). Popper and Munz conjectured that such a view enables a convergence between knowledge and organisms because organisms become understood as unfalsified theories about an outer world, and theories become understood as evolving organisms. That is, traditional evolutionary epistemologists on the one hand understand evolving organisms as nature's way to conjecture theories about the world that than either become rejected by the environment when maladaptive, or selected when adaptive; and on the other hand, selection theory becomes applied to knowledge theories that are understood as historical entities that undergo evolutionary change through time. Because selection eliminates the unfit, evolution is understood by traditional evolutionary epistemologists as progressive: organisms become more adapted to their environment and theories become more adept at describing the world.

In what regards the *epistemology of evolution*, traditional evolutionary epistemologists have helped to expand the Neo-Darwinian framework by contemplating the nature of natural selection (Bradie 1986; Campbell 1974a; 1997) and by contributing to the units and levels of selection debate (Brandon 1982; Dawkins 1976; 1982; Hull 1980; 1981; Lewontin 1970; Lloyd 1988) that gave way to multilevel selection theory (Okasha 2006; Plotkin & Odling-Smee 1981). These endeavors have enabled an expansion of the Neo-Darwinian framework to non-biological domains, including epistemology, and it has led to the founding of Universal Darwinism (Dawkins 1983) and Universal Selection Theory (Cziko 1995).

Afterwards, the universalization of selection theory toward all domains of life and the universal endorsement of adaptationist and gene-centered approaches to evolution and knowledge were criticized in the cognitive (Piaget 1971) and biological sciences (Gould & Lewontin 1979) and countered by the adoption of a general systems outlook (von Bertalanffy 1950). These schools emphasize the creative role organisms play in shaping their development and their environment through learning (Piaget 1971), self-organization (Maturana 1978), and niche construction (Lewontin 1983a, b; von Uexküll 1921). In the sociocultural sciences, gene-reductionist views were complemented by dual inheritance or gene-culture co-evolutionary theories (Boyd & Richerson 1985; Feldman & Cavalli-Sforza 1976).

These new research directions affected theorizing on the *evolution of epistemology* through the introduction of systems-theoretical (Hahlweg & Hooker 1989), constructivist (Diettrich 2004; 2006; Riegler 2006; von Glaserfeld 2001), and non-adaptationist EEs (Wuketits 1990; 2006). These EEs favor constructivist worldviews over adaptationist ones, and coherence theories over hypothetical realist worldviews. Self-organization and niche construction emphasize the active role organisms play in directing their own behavior and in organizing and creating their environment, sometimes, as Lewontin (1983b) argued, despite the environmental selection they are passively subjected to. This suggests that evolving knowledge be understood not as necessarily true or corresponding to an outer world, but as functional for the organism in the inner cognitive world or niche it constructs for itself (Gontier 2006; Facoetti 2019; Facoetti & Gontier 2021, forthcoming).

Through the organism-focused, system theoretical approaches to EE, adherents of this school have also helped advance theorizing on the *epistemology of evolution*. In this research area, they have contributed to the foundation of the current Eco-Evo-Devo schools (Abouheif et al 2014; Gilbert & Epel 2008; Gould 1977; West-Eberhard 2003) that associate with the plea for an Extended Evolutionary Synthesis (Pigliucci 2009; Pigliucci & Müller 2010), and scholars have also contributed to theorizing on the major transitions in evolution (Maynard Smith & Szathmáry 1995).

Conflicts between reductionist and dialectic or holistic approaches have furthermore brought to light the importance of developing hierarchy (Pattee 1973; Riedl 1984; Salthe 1985; Simon 1962) and causality theories (Campbell 1974b; Emmeche et al. 2000). Both approaches accept the existence of upward or bottom-up causation (Craver & Bechtel 2007; Rosenberg 2020), but they remain divided over the existence and relevance of downward or top-down causal processes (Campbell 1974b, 182; 1990; Emmeche et al. 2000; Paoletti & Orilia 2017).

Debates on the range of the Modern Synthesis and its possible extensions (Table 3) are nowadays further intensified due to the important insights coming in from molecular genetics (Woese 1998) and mobile DNA studies (Shapiro 2011), epigenetics (Hallgrímsson & Hall 2011; Jablonka & Lamb 1995), physiology (Noble 2012), reticulate evolution studies (Doolittle 2010; Gontier 2015; Margulis 1991; Sapp 1994), research on ecological and genetic drift (Hubbell 2001; Kimura 1983), macroevolutionary theories (Eldredge & Salthe 1984; Eldredge 1985; Gould & Eldredge 1977; Serrelli & Gontier 2015; Vrba & Gould 1986), and biophysics (Salthe 1985; Zhou 2011). These further complexify the ongoing debates on the nature of causality by demonstrating the existence of multiple evolutionary mechanisms and processes; and they complexify the debates on evolutionary hierarchies (Hull 1980; 1981) by proving that multiple hierarchies can be distinguished (Eldredge 1985) and that a myriad of reticulate interactions occur within and between these

Table 3 Beyond the Modern and Extended Evolutionary Synthesis

The evolutionary epistemological foundations of the Modern Synthesis		
What evolves: *Organism* (genetic traits) => Unit *Where* evolution occurs: A/biotic *environment* => Level *How* evolution occurs: Environmental (natural and sexual) *selection* and drift (understood as a period of no selection) = > Mechanism		
Pigliucci and Müller's (2010, 11) characterization of "key concepts" that underlie a three-phased expansion of evolutionary theory toward an "Extended Evolutionary Synthesis"		
I Darwinism	II The Modern Synthesis	III The Extended Evolutionary Synthesis
• Variation • Inheritance • Natural selection	• Genetic mutation • Mendelian inheritance • Population genetics • Contingency • Speciation & trends	• Evo-Devo theory • Plasticity & accommodation • Niche construction • Epigenetic inheritance • Replicator theory • Evolvability • Multilevel selection • Genomic evolution
Evolutionary theories that have identified additional units, levels, and mechanisms of evolution		
• Biochemical and molecular (epi)genetic theories including gene mobility, organellar, and cell theories • Physiological (system) theories • Genetic & ecological drift theories • Ecological theories • Reticulate evolution theories (symbiosis, symbiogenesis, lateral gene transfer, infective heredity, hybridization) • Behavioral and cognitive learning theories • Sociocultural and linguistic evolution theories • Technological evolution theories • Biophysics theories		

hierarchies (Gontier 2018a, b). This has brought forth a new wave where the principles and techniques of traditional evolutionary epistemological approaches have become abstracted and *applied* to the numerous evolutionary theories that exist today.

Applied Evolutionary Epistemology (Gontier 2010; 2012; 2017; 2018c) is a philosophical theory and a scientific methodology that aims to identify and study the ontological structures foundational for biological, sociocultural, linguistic, and technological evolution and theorizing thereof. To that end, it analyzes how a plurality of units, levels, mechanisms and processes causally bring forth hierarchically-structured evolving realities that display diverging and converging patterns in the mode and tempo of their evolution.

Concerning *the evolution of epistemology*, applied EE (Gontier 2018c) has come to reject the idea that there is a single reality or a world as it is in itself. Thinking through the consequences of traditional EE that already synthesized organisms with epistemology, as well as the consequences of cognitive and environmental niche construction theory that founded non-adaptationist EE, and by integrating the important insights coming in from the new evolutionary sciences, Gontier (2018c) has demonstrated that the epistemology-ontology divide has become untenable. Rather than adhering to the existence of an abiotic world in itself that somehow dissociates from a biotic world, applied EE understands organisms as constructors of spatiotemporally-bounded biorealities (Gontier & Bradie 2017). That means that if there once was a division between life and a physical world as it is in itself, that world has since evolved into a living earth. The spatiotemporal aspect of evolution moreover annihilates the idea that there exists a single reality. What is real changes over time. Because life evolves and because it constantly builds new habitable zones of life, what counts as real and true is spatiotemporally bounded to a specific bioreality, and epistemology equals ontology in time and space (Gontier 2018c).

Regarding the *epistemology of evolution*, recognizing unit and level plurality paved the way for recognizing mechanism and process plurality (Gontier 2010). Beyond debating the nature of universal units and levels of selection in particular, as well as attempts to abstract the universal heuristic or logical skeleton whereby selection operates at all domains of life, Gontier (2018a) has suggested that an even more fundamental structure pertains to all evolutionary epistemologies and to all evolutionary processes. Namely, all forms of evolution, whether they occur by natural selection or by other means, proceed by units that evolve at levels by mechanisms and processes. Of importance therefore is the question how these multiple units, levels, and mechanisms and processes interact reticulately and how they causally bring forth hierarchically-structured ontological biorealities that are bounded in space-time.

As this review of the three evolutionary epistemological schools comes to conclusion, it becomes obvious that although the schools have worked from within different and evolving evolutionary paradigms, they are joined by their mutual interest in unravelling the nature of knowledge and the nature of evolution. The two research avenues are thereby tightly connected to one another. Knowledge is dependent upon the biologically evolved ability to cognize; the socio-culturally evolved means to store, transmit, accumulate or revise information and knowledge; and the evolutionary development of technological means that enable to go beyond existing knowledge. And knowledge on how epistemology evolves is dependent upon evolutionary theories. Both research avenues moreover hold a shared agenda in trying to uncover the hierarchical and causal nature of ontology through epistemology (Table 4).

By generalizing the procedures followed by scholars that universalized Darwinism, and by applying them to evolutionary mechanisms and processes beyond selection theory, applied EE is the only school that recognizes the plurality of all elements (units, levels, mechanisms and processes, and evolutionary hierarchies) under study.

3 Current Approaches

Beyond this introduction, this special issue contains nine papers written by scholars actively engaged with issues in evolutionary epistemology. Contributing authors focus on the impact interactional, non-adaptationist, and constructivist approaches have on classic epistemology-ontology divisions, and how this brings forth new theorizing on causality and hierarchy theories.

Marta Facoetti (2019) reviews how adherents of non-adaptationist and constructivist approaches to EE, such as Wuketits (2006), Diettrich (2004), and Riegler (2006), understand the organism-environmental relationship in dialectical terms. She investigates how these views negate the idea, still defended by adherents of traditional, adaptationist EE, that, ontologically, there exists a world-in-itself, and epistemologically, organismal knowledge corroborates or

Table 4 EE's Shared research agenda

• Identifying unit/s, level/s, mechanism/s and process/es of evolution
• Developing hierarchy & causality theories
• Understanding bioreality/ies

corresponds to truth. Instead, she examines the various moderate forms of realism proposed by non-adaptationist EE-ers, including Wuketits' (2006) functional realism, Ruse's (1989) common-sense realism, Clark's (1986) non-realism, and von Glasersfeld's (1991) radical constructivism.

Predrag Slijepčević (2019) understands learning as a universal capacity that underlies constructivism. He continues the original expansion of evolutionary epistemology toward ethological research by investigating how biological organisms other than humans qualify as knowers. Innovative about his approach is that he investigates how knowers also extend the animal kingdom and how cognition is already present in bacteria. All life forms, from bacteria onward, demonstrate a natural capacity to learn. Learning is no longer understood as a form of imprinting, but as an interactional process. Building on the works of Bateson (1979) and Corning (2007), he thereby updates Plotkin's and Odling-Smee's (1982) concept of natural learning. For Slijepčević, learning reflects a capacity to control or gain, process, and translate information. This algorithm is universal and functions as the foundation for communicative interactions between systems that range from simple cells to ecosystems.

C. David Suárez Pascal (2021) compares Hanson's (1960) theory on the logic of discovery and his understanding of theories as extensions of organismal physiology with von Uexküll's (1921) theories on the relationship between organisms and their environments and goes on to present a biosemiotic (Kull et al., 2009) concept of human scientific theories relevant for evolutionary epistemology and for how it understands the ontology-epistemology divide. For classic evolutionary epistemologists, organisms and their cognitive and physiological properties can be understood as theories of the world and there is thus a convergence between the biological world and epistemology. Suárez thereby goes on to investigate the status of human scientific knowledge in general and abductive or hypothesis-generating reasoning in particular. For Suárez, scientific knowledge is inherently symbolic due to its use of language and mathematics, and this implies a form of semiosis between the symbolic and iconic (sensorial). This then is what suggests creativity and choice.

Lorenzo Magnani (2019) also examines abductive or hypothetical reasoning in humans, and he does so by understanding it as an example of cognitive niche construction. He thereby points toward the pioneering work of Herbert Simon (1955) on incomplete information processing. As chance seekers, Magnani details, humans are ecological engineers that actively modify and build their environment rather than that they adapt to it as traditional evolutionary epistemologists proclaimed. Niche construction moreover demonstrates the existence of an ecological inheritance system (Odling-Smee 1988) that complements the genetic inheritance system. For Magnani, and by following Hutchins (1995), this ecological inheritance system is based upon distributed cognition. Through cognitive niche construction, humans create the environment where natural selection occurs, and following Turner (2004), this demonstrates a sense of purposefulness and directionality to the course of evolution.

Human creativity and biological directionality are also examined by *Denis Noble and Raymond Noble* (2020). The scholars investigate how physiologically, organisms can demonstrate intentional agency characterized by rational, value-driven actions and creativity that surpass their genetic and molecular endowment. As an instance of what Denis Noble (2012) calls "biological relativity", organisms can harness stochasticity at molecular, cellular, organismal, and social levels in ways that it underlies choice, and choice can provide directionality to evolution. Such directionality requires a holistic, top-down or what they call macro-level causal analysis of behavior. The Nobles thereby side with Karl Popper (in Niemann 2014; Popper & Eccles 1977) who recognized an active part to Darwinian theory, while they counter Kim's (2000) defense of physicalism that instead argues for causal closure at a micro-level or what Popper characterized as passive Darwinism, i.e. a reductionist Darwinism that denies macro-level causation or free will.

Non-adaptationist, constructivist, and biosemiotic approaches surpass the tenets of the Modern Synthesis and these schools of thought have helped raise awareness on the important role played by developmental and ecological processes in evolution. These ideas are foundational for the Extended Evolutionary Synthesis that emphasizes the importance of an Eco-Evo-Devo approach to evolution (Pigliucci & Müller 2010). In line with this tradition, *Isabella Sarto-Jackson* (2019) analyses how the EEM program that gave way to the current field of cognitive biology (Kovac 2000) has evolved to also include developmental research; and how the EET program, through the adoption of niche construction theory, expanded toward ecological approaches (Laland et al. 2016; Lewontin 1983a, b). Sarto-Jackson (2019), and herein following Maynard Smith et al. (1985) as well as Riedl (1978), Arthur (2001), and Gilbert (2010), discusses how scholars can in particular research developmental constraints and how these constraints in turn can be understood as developmental drives. She therefore emphasizes the need for a multi-level hierarchical perspective that recognizes both up- and downward causation.

Building upon the works of Simon (1962) and Mayr (1982), *Nathalie Gontier* (2021) points toward the intricate relation that exists between hierarchy and causality thinking within the evolution of science in general and within the evolutionary sciences in particular. Working from within macroevolutionary (Eldredge 1985) and reticulate evolutionary schools of thought (Gontier 2015), she goes beyond the classic debate on the dialectics of upward and downward causation (Campbell 1974b), and she points towards the existence of reticulate causal processes that occur within and between evolutionary hierarchies. She furthermore links reticulate causal theories to the rise of statistical network-thinking and outlines how both require a reevaluation of classic ontological hierarchy theories.

The following two authors dig deeper into current statistical thinking and how it is applied within evolutionary epistemology in general and cultural evolution studies in specific. *Pierre Poirier, Luc Faucher, and Jean-Nicolas Bourdon* (2019) plead for more pluralism in cultural evolution theories by investigating epistemic systems and how they relate to the world. Following Quine's (1969) ideas on the evolutionary need for inductive achievements to be efficient, they define epistemic systems as "systems capable of "'truth-tracking', that is, able to form true beliefs about their environment." But against older adaptationist ideas defended by Dretske (1981), Millikan (1984), and Sterelny (2003), they do not understand such truth-tracking to involve reconstructions of reality. Instead, and thereby following Clark (2016), they understand truth-tracking to involve the making of adjustable predictions on, and inferences of reality, which they analyze as "Bayesian belief updating" and Markov Blankets. They thereby follow Campbell (2016) who understands Bayesian Inference as foundational for Universal Darwinism. By building on the work of Laudan (2006), they go on to examine justice systems as examples of such truth-tracking epistemic systems.

Antonio Fadda (2020) analyses cultural evolution theories as they are proposed by evolutionary psychologists such as Cosmides et al. (2010), Henrich and McElreath (2003), Mesoudi et al. (2013), Boyd and Richerson (1985), and Claidière and Sperber (2007). These scholars propose to incorporate the field of evolutionary epistemology into their area of research by understanding individual cognition and epistemic evolution as aspects of and thus as part of cultural evolution studies. He compares the current population rather than trait-based accounts of scientific diversity to the classic approaches within EET as they were proposed by Campbell (1965), Toulmin (1967), and Hull (1988), and he points out how both programs can be improved by also including sociological perspectives on knowledge (Kitcher, 1990).

4 Concluding Remarks

Originally focused on unravelling the evolution of knowledge and information in both human and other animals, as well as how that knowledge relates to the world as it is in itself, EE developed into two related research programs, the EEM and EET program. From within the EEM program, scholars initially investigated the cognitive and biological mechanisms relevant for understanding the evolution of knowledge in our and other species; and from within the EET program, scholars investigated how human knowledge in particular, that comes in the form of science, culture and language, evolves. The EEM program has thereby evolved into overall research on the evolution of epistemology, and the EET program has evolved into research on the epistemology of evolution.

Over the years, EE has also helped found disciplinary fields such as ethology, psychology, and cultural evolution studies as well as the field of philosophy of biology. In all cases, EE has sometimes been argued to dissolve into the disciplines and areas of research that it has helped to establish. And while it is certainly true that many of the ideas that originate in EE have been taken as foundational for other disciplines, none of these disciplines so far have been able to fully explain the evolution of epistemology, or the epistemology of evolution, and what such implies for our understanding of ontology. It is therefore safe to say that EE not only maintains autonomy as a discipline, it continues to pioneer in the expansion of both evolutionary and epistemological research.

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References

Abouheif, E., Favé, M. J., Ibarrarán-Viniegra, A. S., Lesoway, M. P., Rafiqi, A. M., & Rajakumar, R. (2014). Eco-evo-devo: The time has come. *Advances in Experimental Medicine and Biology, 781*, 107–125.

Arthur, W. (2001). Developmental drive: An important determinant of the direction of phenotypic evolution. *Evolution & Development, 3*, 271–278.

Bateson, G. (1979). *Mind and nature: A necessary unity*. New York, NY: Bantam Books.

Boyd, R., & Richerson, P. (1985). *Culture and the evolutionary process*. University of Chicago Press.

Bradie, M. (1986). Assessing evolutionary epistemology. *Biology & Philosophy, 1*(4), 401–459.

Bradie, M., & Harms, W. (2020). Evolutionary epistemology. In Zalta, E. N. (Ed.), *The Stanford encyclopedia of philosophy (Spring 2020 Edition).* Available online at https://plato.stanford.edu/archives/spr2020/entries/epistemology-evolutionary (Accessed on May 15th, 2020).

Brandon, R. (1982). The levels of selection. In R. Brandon & R. Burian (Eds.), (1984), *Genes, organisms, populations: Controversies over the units of selection* (pp. 133–139). Cambridge, MA: MIT Press.

Campbell, D. T. (1960). Blind variation and selective retention in creative thought as in other knowledge processes. *Psychological Review, 67*(6), 380–400.

Campbell, D. T. (1965). Variation and selective retention in socio-cultural evolution. In H. R. Barringer, G. L. Blanksten, & R. W. Mack (Eds.), *Social change in developing areas: A reinterpretation of evolutionary theory* (pp. 19–49). Cambridge, MA: Schenkman.

Campbell, D. T. (1974a). Evolutionary epistemology. In P. A. Schlipp (Ed.), *The philosophy of Karl Popper.* (Vol. I, pp. 413–459). Chicago, IL: La Salle.

Campbell, D. T. (1974b). Downward causation in hierarchically organized biological systems. In F. J. Ayala & T. Dobzhansky (Eds.), *Studies in the philosophy of biology* (pp. 179–186). London: Macmillan.

Campbell, D. T. (1990). Levels of organization, downward causation, and the selection-theory approach to evolutionary epistemology. In Greenberg, G., & Tobach, E. (Eds.), *The T. C. Schneirla conference series, Vol. 4, Theories of the evolution of knowing* (pp. 1–17). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Campbell, D. T. (1997). From evolutionary epistemology via selection theory to a sociology of scientific validity. *Evolution and Cognition, 3*, 5–38.

Campbell, J. O. (2016). Universal Darwinism as a process of Bayesian inference. *Frontiers in Systems Neuroscience, 10*(49), 49.

Claidière, N., & Sperber, D. (2007). The role of attraction in cultural evolution. *Journal of Cognition and Culture, 7*, 89–111.

Clark, A. J. (1986). Evolutionary Epistemology and the scientific method. *Philosophica, 37*(1), 151–162.

Clark, A. (2016). *Surfing uncertainty*. Oxford: Oxford University Press.

Corning, P. (2007). Control information theory: The missing link in the science of cybernetics. *Systems Research and Behavioral Science, 2*(3), 297–311.

Cosmides, L., Barrett, H. C., & Tooby, J. (2010). Adaptive specializations, social exchange, and the evolution of human intelligence. *Proceedings of The National Academy of Sciences, 107*, 9007–9014.

Craver, C. F., & Bechtel, W. (2007). Top-down causation without top-down causes. *Biology & Philosophy*, 22, 547–563.

Cziko, G. (1995). *Without miracles: Universal selection theory and the second Darwinian revolution*. Cambridge, MA: MIT Press.

Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.

Dawkins, R. (1982). Replicators and vehicles. In R. Brandon & R. Burian (Eds.), (1984), *Genes, organisms, populations: Controversies over the units of selection* (pp. 161–179). Cambridge, MA: MIT Press.

Dawkins, R. (1983). Universal Darwinism. In D. L. Hull & M. Ruse (Eds.), *The philosophy of biology* (pp. 15–35). Oxford: Oxford University Press.

Diettrich, O. (2004). Cognitive evolution. In F. Wuketits & C. Antweiler (Eds.), *Handbook of evolution* (vol. 1, pp. 25–75). Weinheim: Wiley & Co.

Diettrich, O. (2006). The biological boundary conditions for our classical physical world view. In N. Gontier, J. P. Van Bendegem, & D. Aerts (Eds.), *Evolutionary epistemology, language and culture* (pp. 67–93). Dordrecht: Springer.

Doolittle, F. W. (2010). The attempt on the tree of life: Science, philosophy and politics. *Biology & Philosophy, 25*, 455–473.

Dretske, F. (1981). *Knowledge and the flow of information*. Cambridge, MA: MIT Press.

Eldredge, N. (1985). *Unfinished synthesis: Biological hierarchies and modern evolutionary thought*. New York, NY: Oxford University Press.

Eldredge, N., & Salthe, S. (1984). Hierarchy and evolution. *Oxford Surveys in Evolutionary Biology, 1*, 184–208.

Emmeche, C., Køppe, S., & Stjernfelt, F. (2000). Levels, emergence, and three versions of downward causation. In Andersen, P. B., Emmeche, C., Finnemann, N., & Christiansen; P. (Eds.), *Downward causation: Minds, bodies and matter* (pp. 13–34). Aarhus: Aarhus University Press.

Facoetti, M. (2019). United in diversity: An organic overview of non-adaptationist evolutionary epistemology. *Journal of General Philosophy of Science*. https://doi.org/10.1007/s10838-019-09452-y.

Facoetti, M., & Gontier, N. (2021). Biosemiotics and (applied) evolutionary epistemology: A comparison. In Pagni, E., & Simanke, R. T. (Eds.), *Biosemiotics: The natural foundations of symbolism*. Cham: Springer.

Fadda, A. (2020). Population thinking in epistemic evolution: Bridging cultural evolution and the philosophy of science. *Journal for General Philosophy of Science*. https://doi.org/10.1007/s10838-020-09497-4.

Feldman, M., & Cavalli-Sforza, L. (1976). Cultural and biological evolutionary processes, selection for a trait under complex transmission. *Theoretical Population Biology, 9*(2), 238–259.

Gilbert, S. F. (2010). *Developmental biology*. Sunderland, MA: Sinauer Associates.

Gilbert, S. F., & Epel, D. (2008). *Ecological developmental biology: Integrating epigenetics, medicine and evolution*. Sunderland, MA: Sinauer Associates Inc.

Gontier, N. (2006). Introduction to evolutionary epistemology, language and culture. In N. Gontier, et al. (Eds.), *Evolutionary epistemology, language and culture* (pp. 1–29). Dordrecht: Springer.
Gontier, N. (2010). Evolutionary epistemology as a scientific method: A new look upon the units and levels of evolution debate. *Theory in Biosciences, 129*(2–3), 167–182.
Gontier, N. (2012). Applied evolutionary epistemology: A new methodology to enhance interdisciplinary research between the human and natural sciences. *Kairos, Journal of Philosophy and Science, 4*, 7–49.
Gontier, N. (Ed.). (2015). *Reticulate evolution*. Cham: Springer.
Gontier, N. (2017). What are the levels and mechanisms/processes of language evolution? *Language Sciences, 63*, 12–43.
Gontier, N. (2018a). What are the units of language evolution? *Topoi, 37*(2), 235–253.
Gontier, N. (2018b). On how epistemology and ontology converge through evolution: The applied evolutionary epistemological approach. In S. Wuppuluri & F. Doria (Eds.), *The map and the territory, Foreword by Sir Roger Penrose and afterword by Dagfinn Føllesdal* (pp. 533–569). Cham: Springer.
Gontier, N. (2018c). Cosmological and phenomenological transitions into how humans conceptualize and experience time. *Time & Mind*, *11*(3), 325–335.
Gontier, N. (2021). Hierarchies, networks, and causality: The applied evolutionary epistemological approach. *Journal for General Philosophy of Science*. https://doi.org/10.1007/s10838-021-09565-3.
Gontier, N., & Bradie, M. (2017). Acquiring knowledge on species–specific biorealities: The applied evolutionary epistemological approach. In R. Joyce (Ed.), *Routledge handbook of philosophy of biology* (pp. 136–152). London: Routledge.
Gould, S. J. (1977). *Ontogeny and phylogeny*. Cambridge, MA: Belknap, Harvard University Press.
Gould, S. J., & Eldredge, N. (1977). Punctuated equilibria: The tempo and mode of evolution reconsidered. *Paleobiology, 3*(2), 115–151.
Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings for the Royal Society London, B, 205*, 581–589.
Hahlweg, K., & Hooker, C. A. (Eds.). (1989). *Issues in evolutionary epistemology*. Albany, NY: State University of New York Press.
Hallgrímsson, B., & Hall, B. K. (2011). *Epigenetics*. Berkeley: University of California Press.
Hanson, N. R. (1960). Is there a logic of scientific discovery? *Australasian Journal of Philosophy, 38*(2), 91–106.
Henrich, J., & McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology, 12*(3), 123–135.
Hubbell, S. (2001). *The unified neutral theory of biodiversity*. Princeton, NJ: Princeton University Press. https://doi.org/10.1007/s10838-021-09563-5.
Hull, D. L. (1980). Individuality and selection. *Annual Review of Ecology and Systematics, II*, 311–332.
Hull, D. L. (1981). Units of evolution. In R. Brandon & R. Burian (Eds.), *(1984), Genes, organisms, populations: Controversies over the units of selection* (pp. 142–159). Cambridge, MA: MIT Press.
Hull, D. L. (1988). *Science as a process: An evolutionary account of the social and conceptual development of science*. Chicago, IL: The University of Chicago Press.
Hutchins, E. (1995). *Cognition in the wild*. Cambridge, MA: MIT Press.
Jablonka, E., & Lamb, M. (1995). *Epigenetic inheritance and evolution*. New York, NY: Oxford University Press.
Kim, J. (2000). *Mind in a physical world*. Cambridge, MA: MIT Press.
Kimura, M. (1983). *The neutral theory of molecular evolution*. Cambridge: Cambridge University Press.
Kitcher, P. (1990). The division of cognitive labor. *Journal of Philosophy, 87*, 5–22.
Kovac, L. (2000). Fundamental principles of cognitive biology. *Evolution and Cognition, 6*, 51–69.
Kull, K., Deacon, T., Emmeche, C., Hoffmeyer, J., & Stjernfelt, F. (2009). Theses on biosemiotics: Prolegomena to a theoretical biology. *Biological Theory, 4*, 167–173.
Laland, K. N., Matthews, B., & Feldman, M. W. (2016). An introduction to niche construction theory. *Evolutionary Ecology, 30*, 191–202.
Laudan, L. (2006). *Truth, error, and criminal law*. Cambridge: Cambridge University Press.
Lewontin, R. (1970). The levels of selection. *Annual Review of Ecological Systems, 1*, 1–18.
Lewontin, R. (1983a). Gene, organism, and environment. In D. S. Bendall (Ed.), *Evolution from molecules to men* (pp. 273–285). Cambridge University Press.
Lewontin, R. (1983b). The organism as subject and object of evolution. *Scientia, 188*, 65–82.
Lloyd, E. (1988). *The structure and confirmation of evolutionary theory*. Westport, CT: Greenwood Press.

Lorenz, K. (1941). Kants Lehre vom Apriorischen im Lichte gegenwärtiger Biologie. *Blätter für Deutsche Philosophie, 15*, 94–125.
Lorenz, K. (1958). The evolution of behavior. *Scientific American, 199*(6), 67–78.
Lumsden, C., & Wilson, E. (1981). *Genes, mind and culture: The coevolutionary process*. Cambridge, MA: Belknap, Harvard University Press.
Magnani, L. (2001). *Abduction, reason, and science*. New York: Kluwer Academic/Plenum Publishers.
Magnani, L. (2019). Cognitive niche construction and extragenetic information: A sense of purposefulness in evolution. *Journal for General Philosophy of Science*. https://doi.org/10.1007/s10838-019-09494-2.
Margulis, L. (1991). Symbiogenesis and symbionticism. In L. Margulis & R. Fester (Eds.), *Symbiosis as a source of evolutionary innovation* (pp. 1–14). Cambridge, MA: MIT Press.
Maturana, H. (1978). Biology of language: The epistemology of reality. In G. A. Miller & A. Lenneberg (Eds.), *Psychology and biology of language and thought* (pp. 27–63). New York, NY: Academic Press.
Maynard Smith, J., & Szathmáry, E. (1995). *The major transitions in evolution*. New York, NY: Oxford University Press.
Maynard Smith, J., Burian, R., Kauffman, S., Alberch, S., Campbell, J., Goodwin, B., Lande, R., Raup, D., & Wolpert, L. (1985). Developmental constraints and evolution: A perspective from the Mountain Lake Conference on development and evolution. *The Quarterly Review of Biology*, *60*(3), 265–287.
Mayr, E. (1982). *The growth of biological thought*. Cambridge, MA: Harvard University Press.
Mesoudi, A., Laland, K. N., Boyd, R., Buchanan, B., Flynn, E., McCauley, R. N., Renn, J., Reyes-García, V., Shenan, S., Stout, D., & Tennie, C. (2013). The cultural evolution of technology and science. In Richerson, P. J., & Christiansen, M. H. (Eds.), *Cultural evolution*. Cambridge, MA: MIT Press.
Millikan, R. (1984). *Language thought and other biological categories*. Cambridge, MA: MIT Press.
Munz, P. (1993). *Philosophical Darwinism*. London: Routledge.
Niemann, H.-J. (2014). *Karl Popper and the two new secrets of life*. Mohr Siebeck: Tübingen.
Noble, D. (2012). A theory of biological relativity: No privileged level of causation. *Interface Focus, 2*, 55–64.
Noble, R., & Noble, D. (2020). Can reasons and values influence action: How might intentional agency work physiologically? *Journal for General Philosophy of Science*. https://doi.org/10.1007/s10838-020-09525-3.
Odling-Smee, F. J. (1988). *The role of behavior in evolution*. Cambridge: Cambridge University Press.
Okasha, S. (2006). *Evolution and the levels of selection*. Oxford: Oxford University Press.
Paoletti, M. P., & Orilia, F. (Eds.). (2017). *Philosophical and scientific perspectives on downward causation*. London: Routledge.
Pattee, H. (Ed.). (1973). *Hierarchy theory: The challenge of complex systems*. New York, NY: George Braziller.
Piaget, J. (1971). *Genetic epistemology*. New York, NY: W. W. Norton.
Pigliucci, M. (2009). An extended synthesis for evolutionary biology. *Annals of the New York Academy of Sciences, 1168*, 218–228.
Pigliucci, M., & Müller, G. (Eds.). (2010). *Evolution: The extended synthesis*. Cambridge, MA: MIT Press.
Plotkin, H., & Odling-Smee, F. (1981). A multiple-level model of evolution and its implications for sociobiology. *Behavioral and Brain Sciences, 4*(2), 225–235.
Plotkin, H. C., & Odling-Smee, F. J. (1982). Learning in the context of a hierarchy of knowledge gaining processes. In H. C. Plotkin (Ed.), *Learning, development and culture: Essays in Evolutionary Epistemology* (pp. 443–471). New York, NY: John Wiley & Sons.
Poirier, P., Faucher, L., & Bourdon, J. N. (2019). Cultural blankets: Epistemological pluralism in the evolutionary epistemology of mechanisms. *Journal for General Philosophy of Science*. https://doi.org/10.1007/s10838-019-09472-8.
Popper, K. (1963). *Conjectures and refutations*. London: Routledge & Kegan Paul.
Popper, K. R. (1972). *Objective knowledge. An evolutionary approach*. Oxford: Oxford University Press.
Popper, K., & Eccles, J. C. (1977). *The self and its brain*. Berlin: Springer.
Provine, W., & Mayr, E. (Eds.). (1980). *The evolutionary synthesis: Perspectives on the unification of biology*. Belknap: Harvard University Press.
Quine, W. V. (1969). *Ontological relativity and other essays*. New York, NY: Columbia University Press.
Riedl, R. (1978). *Order in living organisms: A systems analysis of evolution*. New York, NY: Wiley.
Riedl, R. (1984). *Biology of knowledge: The evolutionary basis of reason*. Chichester: John Wiley & Sons.
Riegler, A. (2006). Like cats and dogs: Radical constructivism and evolutionary epistemology. In N. Gontier, J. P. Van Bendegem, & D. Aerts (Eds.), *Evolutionary epistemology, language and culture* (pp. 47–65). Dordrecht: Springer.
Rorty, R. (1980). *Philosophy and the mirror of nature*. Oxford: Blackwell.

Rosenberg, A. (2020). *Reduction and mechanism*. Cambridge: Cambridge University Press.
Ruse, M. (1986). *Taking Darwin seriously*. Oxford: Blackwell.
Ruse, M. (1989). The view from somewhere: A critical defense of evolutionary epistemology. In K. Hahlweg & C. A. Hooker (Eds.), *Issues in Evolutionary epistemology* (pp. 185–228). Albany, NY: State University of New York Press.
Salthe, S. N. (1985). *Evolving hierarchical systems*. New York, NY: Columbia University Press.
Sapp, J. (1994). *Evolution by association: A history of symbiosis*. New York, NY: Oxford University Press.
Sarto-Jackson, I. (2019). Converging concepts of evolutionary epistemology and cognitive biology within a framework of the extended evolutionary synthesis. *Journal for General Philosophy of Science*. https://doi.org/10.1007/s10838-019-09479-1.
Serrelli, E., & Gontier, N. (Eds.). (2015). *Macroevolution*. Cham: Springer.
Shapiro, J. A. (2011). *Evolution: A view from the 21st century*. Upper Saddle River, NJ: FT Press.
Simon, H. A. (1955). A behavioral model of rational choice. *The Quarterly Journal of Economics, 69*, 99–118.
Simon, H. A. (1962). The architecture of complexity. *Proceedings of the American Philosophical Society, 106*(6), 467–482.
Skinner, B. F. (1981). Selection by consequences. *Science, 213*, 501–504.
Slijepcevic, P. (2019). Principles of information processing and natural learning in biological systems. *Journal for General Philosophy of Science*. https://doi.org/10.1007/s10838-019-09471-9.
Sterelny, K. (2003). *Thought in a hostile world*. New York, NY: Wiley-Blackwell.
Suárez Pascal, C. D. (2021). N. R. Hanson and von Uexküll: A biosemiotic and evolutionary account of theories. *Journal for General Philosophy of Science*. https://doi.org/10.1007/s10838-021-09552-8.
Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie, 20*, 410–433.
Toulmin, S. (1967). The evolutionary development of science. *American Scientist, 57*, 456–471.
Toulmin, S. (1972). *Human understanding*. Princeton, NJ: Princeton University Press.
Turner, J. S. (2004). Extended phenotypes and extended organisms. *Biology and Philosophy, 19*, 327–352.
Vollmer, G. (1975). *Evolutionäre Erkenntnistheorie*. Stuttgart: Hirzel.
Von Bertalanffy, L. (1950). An outline of general systems theory. *British Journal for the History of Science, 1*(2), 134–162.
von Glasersfeld, E. (1991). Fiktion und Realität aus der Perspektive des radikalen Konstruktivismus. In F. Roetzer & P. Weibel (Eds.), *Strategien des Scheins* (pp. 161–175). München: Klaus Boer.
von Glaserfeld, E. (2001). The radical constructivist view of science. *Foundations of Science, 6*(1–3), 31–43.
Von Uexküll, J. (1921). *Umwelt und Innenwelt der Tiere*. Berlin: Springer.
Vrba, E., & Gould, S. J. (1986). The hierarchical expansion of sorting and selection: Sorting and selection cannot be equated. *Paleobiology, 12*, 217–228.
West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford: Oxford University Press.
Woese, C. (1998). The universal ancestor. *Proceedings of the National Academy of Sciences, 95*(12), 6854–6859.
Wuketits, F. M. (1990). *Evolutionary Epistemology and its implications for humankind*. Albany, NY: State University of New York Press.
Wuketits, F. (2006). Evolutionary epistemology: The non-adaptationist approach. In N. Gontier, J. P. van Bendegem, & D. Aerts (Eds.), *Evolutionary epistemology, language and culture* (pp. 33–46). Dordrecht: Springer.
Zhou, H. (2011). Q&A: What is biophysics? *BMC Biology, 9*, 13.