Natural Selection Among Replicators, Interactors and Transactors

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Abstract - In evolutionary biology and ecology, ontological and epistemological perspectives based on the replicator and the interactor have become the background that makes it possible to transcend traditional biological levels of organization and to achieve a unified view of evolution in which replication and interaction are fundamental operating processes. Using the transactional perspective proposed originally by John Dewey and Arthur Fisher Bentley, a new ontological and methodological category is proposed here: the transactor. The transactional perspective, based on the concept of the transactor, bridges the dichotomy between organisms and environment that characterizes the interactional perspective on evolution and provides epistemological support for the emergentist, systemic view of evolutionary and developmental processes.

Keywords - Arthur Fisher Bentley, emergence, hierarchy, holism, interaction, interactor, John Dewey, natural selection, replicator, self-action, transaction, transactional framework, transactor

Introduction

The traditional hierarchy of genes, organisms, populations and species, which for a long time formed the imaginative ontological scenery of evolutionary biology, has undergone a deep metamorphosis in the past two decades. Among scientists who are more sensitive to the epistemological dimension[1] of their work, all these entities are now viewed through the interpretative filter of replication and interaction. Replication concerns the passage of genic information from generation to generation, while the interactive dimension of evolution concerns the interaction of elements on all the organizational levels, from genes to species, with their respective environments. Evolution, in the final analysis, would essentially amount to a problem concerning the dynamics involving both of these processes.

While both the scientific and the philosophical communities commonly accept that the replication dimension of evolution is essentially genic, there is debate over what meaning is to be attributed to the replication and interaction processes. Some endorse a "replicator" perspective, claiming that natural selection occurs essentially at the level of the gene (Dawkins 1989 [1976]; 1999 [1982]). Others endorse an "interactor" perspective and maintain

[1] With "epistemology," here and hereafter in the paper, I mean the part of philosophy that studies the extent and validity of the presuppositions and foundations (ontological, theoretical, methodological) of a specific scientific discipline.

that, while genes participate as mechanisms through which the organism's characteristics are passed on from generation to generation, this does not necessarily mean that the environmental factors causing the differential reproduction and transmission of genes operate at the genic level (Sober 1984). Still others argue in a more positive vein that the evolutionary process operates on organismic and even higher and more inclusive levels such as populations, demes, and species (Wynne-Edwards 1962; 1991; Ruse 1980; Wilson 1980; Sober and Wilson 1998; Oyama 2000; Gould 2002).

My primary objective in this paper is to suggest that the concept of "transactor" can assist in overcoming the traditional ontology of the biological organizational levels (genes, organisms, populations, species) by replacing this with a more general hierarchy that better represents the underlying structure of evolutionary processes. In order to make this point, I will rely on the work of John Dewey and Arthur Fisher Bentley. They identified three stages in the evolution of knowledge, which involve a gradual process of differentiation into self-actional, interactional, and transactional perspectives (Dewey and Bentley 1989 [1949]).

The emergence of the "replicator" and "interactor" perspective in evolutionary biology can be considered to represent Dewey and Bentley's self-actional and interactional perspective, respectively. My proposal of a "transactor" perspective is meant to complete the triad, and open up evolutionary biology for a more systemic, truly holistic epistemological perspective.

It was only after coming up with the term 'transactor' while reading Hull that I became aware that the term had been used at least once by Dewey and Bentley in their writing: "Under present postulation Actor should always be taken as postulationally transactional, and thus as a Trans-actor" (Dewey and Bentley 1989, 259-260). As for the term 'interactor', it occurs in a letter from Bentley to Dewey (November 11, 1943, in Ratner and Altman 1964, 188): "You had '*inter*action' and 'field' and 'interactor' in [your 1925] perception paper." The paper in question is "The Naturalistic Theory of Perception by the Senses" (Dewey 1925). In reality, contrary to Bentley's affirmation, the term 'interactor' does not appear in this paper, even though an interactional perspective on the nature of perception is outlined. However, the meaning proposed in this paper of the term 'transactor' does not cover the same semantic field as the meaning proposed by Dewey.

The epistemological triad: self-action, interaction and transaction

On the basis of the correspondence that Dewey and Bentley maintained for almost twenty years (1932-1951), they wrote several papers conjointly or separately that were published in *The Journal of Philosophy* from 1945 to 1948. These papers were gathered and published in a book *Knowing and the Known* in 1949, with a preface, a few changes and revisions, and one new chapter (Dewey and Bentley 1989 [1949]). In this last phase of his thinking, Dewey collaborated with Bentley in developing what could be defined as a sort of epistemological revolution that was aimed at demolishing one of the main ontological rigidities at the foundation of traditional theories of knowledge. As part of this effort, he proposed "to convert all the *ontological*, as prior to inquiry, into the *logical* as occupied wholly and solely with what takes place in the conduct of inquiry as an ever going concern" (Dewey and Bentley 1989, 287; emphasis in original). The first undisputed assumption of traditional theories of knowledge is that a knowing mind is to be considered independent of the object to be known. This position should not be confused with idealism. On this subject, Dewey recognized that idealist philosophical systems do not accept a separation between the one who knows and the entity known, but he argued that, after having affirmed this, these systems "contradict their own aim by retaining the mental and then swallowing everything else up in it" (Dewey in a letter to Bentley, February 1, 1944, in Ratner and Altman 1964, 208).

Dewey and Bentley proceeded to a historical and evolutionary analysis of the several forms that have characterized scientific inquiry and the various types of knowledge. In their view, three perspectives or levels of inquiry historically follow one another: those associated with "self-action," with "inter-action," and with "trans-action."

The self-actional perspective is characterized by considering things as possessing powers of their own and as acting under their own power (Dewey and Bentley 1989, 66, 101). More specifically, by self-action Dewey and Bentley mean a "pre-scientific presentation in terms of presumptively independent 'actors,' 'souls,' 'minds,' 'selves,' 'powers,' or 'forces,' taken as activating events" (Dewey and Bentley 1989, 71). Or, in other words: "Self-action: when one feels that if you describe *the actor*, you have done the job" (Bentley in a letter to Dewey, September 11, 1944, in Ratner and Altman 1964, 300; emphasis in the original). One example of a self-actional formulation is pre-Galilean physics (Bentley in a letter to Dewey, September 17, 1944, in Ratner and Altman 1964, 310).

The interactional perspective, instead, occurs "where thing is balanced against thing in causal interconnection" (Dewey and Bentley 1989, 101). Interaction is also described as a "presentation of particles or other objects organized as operating upon one another" (Dewey and Bentley 1989, 71). One example of an inter-actional formulation is Newtonian physics (Bentley in a letter to Dewey, September 17, 1944, in Ratner and Altman 1964, 310). However, they noticed the tendency, still present in modern science, to produce explanations that amalgamate the self-actional and inter-actional formulations (Dewey and Bentley 1989, 103).

Dewey and Bentley complete their epistemological triad with the transactional perspective, which occurs "when you just can't tell the story or adequately describe either component without implying the other" (Bentley in a letter to Dewey, September 11, 1944, in Ratner and Altman 1964, 300-301). More specifically, the transactional level of inquiry comes up:

> where systems of description and naming are employed to deal with aspects and phases of action, without final attribution to "elements" or other presumptively detachable or independent "entities," "essences," or "realities," and without isolation of presumptively detachable "relations" from such detachable "elements." (Dewey and Bentley 1989, 101-102)

An emblematic example of a transactional formulation is quantum physics (Dewey in a letter to Bentley, May 22, 1950, in Ratner and Altman 1964, 631-632). To avoid the confusing semantic mix between "inter" and "trans," Dewey and Bentley, emphasize the difference in their meanings so as to eliminate any ambiguities: "[…] by confining the prefix *inter* to cases in which "in between" is dominant, and to employ the prefix *trans* where the mutual and reciprocal are intended" (Dewey and Bentley 1989, 264-265, authors' italics; see also Bentley in a letter to Dewey, September 6, 1942, in Ratner and Altman 1964, 125).

It is interesting to note, however, that biological phenomena as a whole are considered the privileged field of action of the transactional approach: "All events to which life (that is, living or being alive) is attributed are transactional" (Dewey in a letter to Bentley, September 8, 1944, in Ratner and Altman 1964, 299). This approach is considered to be a useful method of posing and analyzing problems in the embryological and organic-environmental domains, and above all, wherever the historical component is prevalent (Bentley in a letter to Dewey, February 10, 1946, in Ratner and Altman 1964, 527). Evolutionary processes are characterized by an evident historical component.

Among the main characteristics of the transactional perspective of interest here are the permanently hypothetical aspects of observation and theory (Dewey and Bentley 1989, 47, 267, 292-293), and the refusal of the philosophical fallacy *par excellence*, the "hypostatization of events" (in terms of elements, objects, entities, relations, means, ends) that emerge in the course of inquiry. The fallacy consists of considering these events as ontological entities independently of the context, methods and purposes of the inquiry (Dewey and Bentley 1989, 102-103, 111; Dewey 1938, 149, 171). Moreover, it is interesting to note that, even when considering what we now call emergent phenomena as factual aspects of biotic and abiotic processes, Dewey and Bentley show a definite epistemological reticence to accept some "doctrines" of the levels of organization de-coupled from the methods and the techniques that have contributed to determining them (Dewey in a letter to Bentley, April 21, 1945, in Ratner and Altman 1964, 403; see also Dewey in a letter to Bentley, June 20, 1945, in Ratner and Altman 1964, 426-427).

To summarize Dewey and Bentley's epistemological proposition, it is particularly interesting to emphasize the substantial difference that exists between the interactional and transactional approaches. The former attributes an intrinsic value to "elements" or "entities" which have "relations", i.e. interact with other elements, entities or the environment (meant as something external to the entity of reference). The transactional approach adopts as a reference entity the "whole" of the events, without identifying the eventual "entities" and the surrounding environment as things that are ontologically separated and subsequently are found to have relationships. In a transactional perspective, it is the intrinsic relationships existing among the ensemble of the factors or entities that generate their specific characteristics: the latter are not intrinsic properties residing in the entities or elements, but are instead continuously produced in the course of the transactional relations.

According to a transactional approach, the distinction between an organism and environment, or the distinction between the elements of the organism and that same organism, is thus not ontological, but purely methodological, in the sense that it depends on our methods of analysis. Therefore, to consider certain distinctions "in knowledge" as separating "real and independent entities" is equivalent to reifying the results of the analysis and supporting a self-actional or interactional metaphysical approach. This hypostatization of the ideational instruments of research would risk transferring specific results obtained in specific domains of inquiry into wider domains and attributing a general value to them.

Replicators and interactors

The replication and interaction processes have been materialized in the "replicator" and "interactor" entities. At first, these terms can appear to be bizarre neologisms concocted to illustrate entities that have complementary roles in evolutionary processes. But I suggest that the picture becomes clearer if another atypical term is added: the "transactor." In order to understand the potential epistemological relevance of this concept, an analysis of the concepts of "replicator" and "interactor" is required first, to which I will proceed now.

The Dawkinsian epistemological groundwork for the replicator concept is the perspective that has emerged from the modern synthesis of evolution, and more particularly from the work of Ronald Aylmer Fisher and George Christopher Williams. Fisher claimed that, as Mendelism localizes the physical basis of inheritance, "the individual genes pass from generation to generation entire and unchanged" (Fisher 1924, 202). This makes it possible to find a mechanism where high mutation rates play an important role in maintaining the stock of genetic variability that determines the speed of evolution, while selection determines the direction of evolution. An epistemological tension between individual and gene-centred perspectives is clearly expressed in Fisher's writings. On the one hand, he maintains that "the principle of Natural Selection […] refers only to the variation among individuals (or co-operative communities), and to the progressive modification of structure or function only in so far as variations in these are of advantage to the individual, in respect to his chance of death or reproduction" (Fisher 1958, 49). On a deeper level, the theoretical core of Fisher's evolutionary perspective remains the single gene, since he clearly considers that, "[e]ach successful gene which spreads through the species, must in some measure alter the selective advantage or disadvantage of many other genes. […] To put the matter in another way, each gene is constantly tending to create genetic situations favourable to its survival, so that an increase in number due to any cause will in its turn react favourably upon the selective advantage which it enjoys" (Fisher 1930, 95). This theoretical position, which focuses on the ontologically fundamental character of genes in the evolutionary process – the fundamental selective significance of genes as the ultimate entities on which selection acts – will find a powerful epistemological echo in the writings of Williams.

Williams, using a perspective that can be defined as "atomistic," considers that only the gene is "an ultimate indivisible fragment" transmitted from one generation to the next (Williams 1966, 24). In explaining adaptation, he asserts that "natural selection arises from a reproductive competition among the individuals, and ultimately among the genes, in a

Mendelian population" (Williams 1966, 251). With regard to the roles of individual selection and the genic dimension in the epistemology of Williams's proposition, we should note that the reference to natural selection at the individual level in his logical argumentation is an epiphenomenon. This is because such a reference always entails the natural selection of alternative alleles in a Mendelian population. Therefore, in the final analysis, Williams's position is that the ontological entity of reference on which selection operates is the gene and not the individual. Secondly, in Williams, as in Dawkins's later work, the formal acknowledgment of the importance of the systematic correlation of the gene in the determination of a character (unity of genotype) is overcome by his ontologically atomistic theory (gene, or allele, as the sole, real entity on which selection operates) and its methodological reductionism. This is expressed in the conviction that an allele can always be characterized by a selection coefficient relative to another allele in the same locus (Williams 1966, 56-57).

But it is difficult to reconcile this with the traditional concept of the genotype as an interactor. Recognizing the genotype unity, on the one hand, and the functional inter-correlation of the genes, on the other, leads to very different conclusions at both the ontogenetic and evolutionary levels. In the latter case, the selection coefficients of the alleles or of the genes are of no great importance, since they represent nothing but a methodological abstraction, or, as claimed by Sober and Lewontin, a mathematical artefact that does not imply an explanation of the causal factors of the selective processes (Sober and Lewontin 1982, 158, 174).[2]

The ontological interactional functionalism is soon forgotten in favor of a methodological reductionism that identifies the adaptations as results of selection acting independently on every locus. In practice, what Williams puts into effect is a kind of feedback of the methodological dimension onto the ontological dimension. An initial formal acknowledgment of the essential functional correlation of genotypes is followed by confirmation of the effectiveness of methodological reductionism, which implies the cancellation of the first assumption.

Similar analytical elements can be found in the constitution of the Dawkinsian replicator concept. In this concept, we can recognize Fisher and Williams's struggle for survival among genes, and a formal acknowledgment of the interactional aspects of the

[2] For a line of thought similar to Sober and Lewontin see also: Wright (1930, 353; reprinted in Provine 1986, 84); Mayr (1963, 278-279); and more recently, Stanford (2001, 224-228); Okasha (2006, 76-111, 125-138).

genotype. According to Dawkins, organisms are survival machines, robots, vehicles blindly programmed to safeguard the existence of selfish genes, otherwise denoted as replicators: "Replicators began not merely to exist, but to construct for themselves containers, vehicles for their continued existence" (Dawkins 1989, 19). Echoing Fisher's race for survival among genes, Dawkins supports a genic selectionism in which the gene-replicator is the basic unit of selfishness, where alleles of the same gene are directly competing with each other for survival. The organisms are, therefore, machines created by genes, which share the characteristic of being a replicator with other molecules. A replicator has "the extraordinary property of being able to create copies of itself" (Dawkins 1989, 15, 35). The genes are discrete entities that come close to the "ideal of indivisible particulateness. A gene is not indivisible, but it is seldom divided" (Dawkins 1989, 33-34, see also 44). Even if the gene-replicators are transmitted from body to body over generations, they must be considered "free and independent agents" (Dawkins 1989, 37, 62; see also El-Hani 2007).[3]

This self-actional perspective cohabits with an interactional one. In fact, genes are highly gregarious and interdependent entities that, in relation to the control of embryonic development, collaborate "in inextricably complex ways, both with each other, and with their external environment." The effect of the genes depends on their genic context and on the environmental context in which the organism develops (Dawkins 1989, 24, 37, 84). The selection of a specific gene depends, according to Dawkins, on its ability to "cooperate with its environment of other genes", and on its compatibility with other genes in the gene pool (Dawkins 1989, 39, 62, 85).

Nevertheless, despite the multi-functionality of the replicator concept – a fundamental, independent agent of evolution and a gregarious element of the genotype – it is still subject to the critique of the self-actional primary assumption. Godfrey-Smith emphasizes that the "official" interactionist affirmations of supporters of genic selectionism go hand-inhand with descriptions of replicators that tend in exactly the opposite direction (Godfrey-Smith 2000, 411-412). Hull clearly identifies the risk of interpreting the replicators-vehicles relation as an asymmetric relation in which the vehicles are "passive tools in the hands of all-powerful replicators" (Hull 1988a, 36). Lewontin emphasizes that when the genes are considered as auto-replicating entities we attribute to them "a mysterious, autonomous power that seems to place them above the ordinary materials of the body" (Lewontin 1991, 48). Griffiths and Gray

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[3] For a conception of "agent" that meets the self-actional view of Dewey and Bentley as well as Dawkins's view of the genes as agents of selection, see Wilson (2005, 6-9, 121-126).

offer a similar criticism of the self-actional tendency of Dawkins's genes: "Genes cannot replicate without an independent inheritance of membranes, centrioles, endoplasmic reticulum and so forth. 'Prime movers themselves unmoved' occur in theology, not in biology" (Griffiths and Gray 1997, 487). In my opinion, the self-actional dimension of the replicator, in the evolutionary dimension, is by far the predominant epistemological aspect that overcomes and overrides the interactional aspect in the ontogenetic dimension.

The self-actional character represents both the force and the weakness of the Dawkinsian replicator view. It is a force, because it has the merit of challenging the predominant organism-centred views of the evolutionary process. This is in part because the identification of a paramount element in the complex web of interrelations and interdependencies among the entities that play a causal role in the processes of natural selection answers a deep need for causal mechanisms in scientific inquiry. On top of that, there is also the psychological need of researchers to be able to refer to discrete, observable, basic entities that are susceptible to manipulation by the imagination and experiment. It is also a weakness, because in the search for this "centre of a radiating field of influence" (Dawkins 1999, 238), Dawkins's self-actional replicator view underestimates the value of other explanatory perspectives, denying *a priori* the possible epistemological and scientific worth of a theoretical pluralism.

An analysis of the interactor concept requires taking into consideration its referential multiplicity. Hull introduced this general concept to avoid the ambiguities intrinsic in the terminology of "units of selection," and attributed to it certain meanings that differentiate it from "replicator." According to Hull, an interactor is "an entity that directly interacts as a cohesive whole with its environment in such a way that replication is differential" (Hull 1980, 318; cf. 1981a, 78; 1988a, 27; 1998, 150).[4] He tried to identify a deeper structural category that permits the abstraction of the traditional ontology of the organizational levels of biology. We could therefore stop referring to individual organisms, populations and other entities, because we could see the evolutionary world in terms of replicators, interactors, and lineages. On the one hand, it could be argued that the purpose of a clearer resolution of this problem was achieved when Hull interpreted cells, organisms, colonies, populations and species as interactors, which he considers "organized wholes that exhibit properties of their own" (Hull 1980, 325). On the other hand, when he uses the term 'interactor' to refer to genes as well

[4] The following definition of interactor more clearly emphasizes the causal role of its environmental interactions with respect to the variability of replication: "an entity that interacts as a cohesive whole with its environment in such a way that this interaction causes replication to be differential" (Hull 2001 [1988b], 109).

(Hull 1980, 325; 1988a, 28, 31; 2001, 47), we have, instead, a polymorphous entity as the gene-replicator-interactor. "Genes of course, can also function as interactors. They interact directly with their cellular environment, but they interact only indirectly with more inclusive environments via the interactors of which they are part" (Hull 1981b, 34). In other words, interactors name the genes and all the remaining organizational levels – with the exception of ecosystems and biotic communities. In passing, it should be noted that Hull also recognizes that, "[w]hen a single structure or entity must perform more than one function, it usually performs none of them very well" (Hull 2001, 111). The gene is of course an entity that essentially interacts at both the genomic and gene pool levels, but the dual use of the gene as replicator and interactor (or interactor's interactor, in the sense of genic-interactor of the interactor-organism) may create semantic ambiguity of the term "interactor" when we compare the references with each other.

For Hull, the term 'individual' can be attributed to any entity that is characterized by its unity and continuity in space-time, in the sense that it is able to maintain its internal organization and cohesion (Hull 1977, 93; 1981, 29).[5] If selection operates on entities that differ from the organism, to be units of selection such entities will have to be "individuals," cohesive wholes, functional wholes, and not groups in the sense of structural wholes, or classes. Selection will have as reference only entities that are "individuals." "Not all individuals can function as units of selection, but only individuals can be selected," and, from this point of view, species must be considered as individuals, in the same way as organisms (Hull 1980, 313).[6] Even if Hull proposes a notion of interacting individuals, he never acknowledges, at least explicitly, the concept of emergent properties. The concept of a cohesive whole can be an aspect of an entity characterized by emergent properties, but it is not sufficient in itself to identify such an entity. Although Hull's use of "individual" as an "organized whole" could lead one to think that he supports an emergentist perspective, his real epistemological position remains, in my opinion, unclear. At any rate, his unconditional

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[5] Concerning the supposed necessary cohesion of the unit of selection, the difference introduced between "response cohesion" and "integrative cohesion" makes it possible to consider some units, for example the species, as entities characterised by response cohesion, but not necessarily by intégrative cohesion (Barker and Wilson 2010, 74-78).

[6] It is worth mentioning that Brandon (1999) contributed to remodelling the evolutionary epistemological landscape by introducing an epistemological differentiation between the syntagms "unit of selection" and "level of selection." The former addresses the question, what entities are reproducing, directly and accurately, their structure, whereas the latter concerns the question, what entities are interacting directly with their environment in a way that leads to differential reproduction (Brandon 1999, 168-171). With the introduction of the concept of "modules of selection" (units of evolutionary transformation), Brandon suggests that from a phenotypical point of view there are "modules" (specific parts or organs of the organism) that evolve quasi-indipendently of other modules or parts (Brandon 1999, 174).

acceptance of the analytical additive approach to explain the fitness of biotic populations or of an organism is not consistent with the classic emergentist view of the evolutionary process (Hull 1980, 1981a).

The transactional Framework

With regard to Hull's specific evolutionary model, the chief peculiarity of his position is its Janus-like character. The interactor concept is currently used to support the existence of evolutionary processes at higher organizational levels, but at the same time the acceptance of gene-based selection (Hull, Langman and Glenn 2001, 51) and an analytical methodology are at the epistemological core of his model. In other words, Hull unambiguously assumes a critical position regarding genic selectionism, which tries to explain all higher-level phenomena based ultimately on references to nothing else but the genes (Hull 1998, 150-151). Yet at the same time his model of evolution as a two-phase process involving replication and interaction can be interpreted as an expansion of a gene selectionist perspective. To maintain the contrary would be equivalent to overriding or denying the pivotal role played by the genic-selectionist perspectives of Williams and Dawkins in the construction of the Hullian evolutionary model.

The interactional perspective proposed by Hull, and now largely accepted by the scientific community, presumes a specific ontological and epistemological picture of reality. The unquestioned underlying assumption is that the environment and the interacting evolutionary entities can be considered as external to each other. The ontological background is dualistic, because in the complex evolutionary process a definitive ontological isolation is supposed to exist between the environment and the entity under selection. Even if, formally, the ontological distinction between an organism and its environment can be considered artificial, it is quickly forgotten in the development of the argument. This distinction has deep repercussions on the scientific and epistemological models.

At this point, the concept of "transaction," as formulated by Dewey and Bentley, suggests itself as the logical complement to Hull's concept of the interactor. A clear, emblematic, intuitive pattern of what a transactor can be is well-represented by the concept of the "ecosystem." It is a configuration of biotic and abiotic dimensions reciprocally affecting or influencing each other in space and time. It is noteworthy that the "fragmentation" of this transactional pattern into "components" with mutual "relations" often implies a changeover to an interactional perspective, a change that usually passes unnoticed. From the evolutionary point of view, this changeover to an interactional perspective means that the population and community dynamics, for example, cannot be understood without reference to the environmental parameters, which constitute with the biotic dimension a single and unique system.

Concerning the population dynamics, the differential proliferation of a population in a biotic community, under any conditions, is “sensitive to” or “dependent on” the environmental context (the term ‘context’ refers to populations of other species or to the energy flows and matter cycles of the abiotic dimension).

More generally, in the debate over selection units, the transactor offers a potential conceptual instrument that is functional with regard to the representation of systemic-emergentist positions concerning the higher levels of organization of the evolutionary process, including populations, communities, and species. Such a preference does not, of course, imply the impossibility of representing lower levels of organization as transactors as well.

The following characteristics qualify the transactor as a potentially useful epistemological entity in the units of selection debate. The transactor is a methodological construct that integrates into the definition of an evolutionary entity those environmental factors that have selective value for its existence. It identifies a functionally cohesive, coherent, complex and relatively independent (or autonomous) environmental-organic entity. Such an entity is part of a transactional, hierarchical web with other entities of similar, lower and higher levels of complexity. In other words, each transactor is constituted by transactors of lower levels of structural and functional complexity, and its identification implies the attribution of specific emergent properties that may express specific adaptations.

More specifically, from a methodological point of view two fundamental aspects have to be pointed out. In the search for the causal explanation of adaptations, we can avoid resorting to the analytic decomposition of the transactor in question into lower level transactors and the successive sum of their properties. The need to take into consideration the upper level transactor is revealed when the differential frequency of the proliferation of an entity (gene, organism, deme, population, species) is sensitive to, or depends on, its ‘context.’

In this latter case, the entity would be the result of an adaptation (or some adaptations) and a selective process intervening at a higher level of organization. With the term ‘context’ I do not want to refer only to the abiotic or biotic environment that surrounds the entity in question. Rather, I am referring to the higher organizational level identifiable with specific emergent properties. In an evolutionary perspective, at least from the organismic level, any level can be considered as an environmental-organic or transactional totality. The transactor concept, as already emphasized, integrates into the definition of an entity those environmental factors that have selective value for its existence. This concerns what Brandon identifies as the "ecological environment" and the "selective environment" (Brandon 1988, 57; 1990, 47, 49; 1992, 81-86). Even if Ernst Mayr was working from a perspective that was not yet totally systemic, he nevertheless illustrated how the "interaction" between the organism and the environment represents the aspect that has the greatest impact on the evolutionary existence or disappearance of a species (Mayr 1963, 7). Wimsatt's definition of the selection unit, for example, holds that an entity may be considered as such only when the variation in its fitness does not depend on the context of the other entities belonging to the same level as the entity in question (Wimsatt 1981, 144). The transactor, instead, postulates more clearly the preponderant influence of downward causation, that is, the influence of the higher organizational levels on the lower ones in the determination of the selective value, the reproductive success, of a specific entity.

Such a methodological construct is useful to grasp how evolution can be considered as a transactional process, in the sense that supposed elements and relations can be fixed, isolated, and considered independent only as a consequence of an abstraction. In other words, through a methodological reification we risk blocking and arresting the co-determining flux of transactors at several levels and the complexities that constitute the evolutionary process.

Furthermore, it is useful to specify that this methodological formalization of the transactor concept does not necessarily involve the rejection of its ontological interpretation. The transactor, in fact, in line with the purposes and preferences of each researcher, has an ontological value whenever the attribution of emergent properties loses its hypothetical character and becomes a character of the entity in question. This character will be considered real and distinctive, though not in absolute terms, but only as regards a specific phase of evolution of the discipline in question. In this case, the methodological conception can be considered as the strong version of the transactor concept and the ontological conception as the weak one.

Transactors on the whole would constitute a transactional hierarchy in which the emergent properties of every level certainly have their 'roots' in a lower level of organization, but also 'take root' in the higher level, since both the higher and lower levels participate in the determination of the emergent properties of a specific level. Moreover, it is important to emphasize that in every type of transactor the environment and the entities, which in a self-actional or interactional perspective have external relations, would instead be considered directly and closely integrated, or connected. In this respect, it is important to notice that Hull too recognizes that "the distinction between an organism and its environment is […] artificial" (Hull 1979, 429; cf. Sober 1984, 87). The theoretical core of a transactional perspective is the idea that there is a strict connection existing 'within' the transactor between the entity selected and the ecological selective environment. The environment is not set definitively once and for all, but is constructed by the organisms at least as much as the same environment contributes to constructing the organisms themselves.

For instance, the genome is the immediate environment of the single gene, or of a complex of genes, and the ontogenetic and evolutionary values of a gene are determined to be an integral part of such an entity. Similarly, as far as the other organizational levels are concerned, they will be organic-environmental entities, like transactors. The biotic and abiotic components of ecosystems that have selective values for the transactor in question must be considered parts of the evolutionary connotation of the individuals, the populations, the communities, and the species. Therefore, in such a perspective, we could speak of transactional emergentism, meaning that the gene is a transactor in comparison to the nucleotides that compose it, the genome in comparison to the genes, a population in comparison to the individuals, and a species in comparison to the populations that make it up. Moreover, the fitness of such entities depends both on specific selective-environmental factors and on the specific properties of the entities in question.

Hierarchy, emergence and transaction

It has gradually become clear that a hierarchical perspective on nature and the evolutionary process is part of a worldview that is capable of generating testable scientific hypotheses in evolutionary biology, ecology, and paleontology. One preliminary observation is that, regardless of the author considered, the central conceptual element joining the different hierarchical views of the evolutionary process is the notion of emergence and its various fields of application. At least three areas can be distinguished where the emergence issue is relevant: ontology, methodology and theoretical domains.

From an ontological perspective, the explicit antithesis between supporters of reductionism and of emergentism takes the form of a sort of bet regarding the nature of the real. Some consider emergence as an actual phenomenon, while others maintain that it is a pseudo-phenomenon observation and analysis employed and from the incompleteness of the theories. From the perspective of methodological emergentism, it is not possible to explain or predict the characteristics belonging to a specific level of organization from the characteristics of a lower level of organization. Put more simply, the study of the parts of an entity and of their interactions is not sufficient to explain or predict all the characteristics of the entity in question. Or, in contrast to Sober's famous quote (Sober 1981, 93), I would say: "the whole is above and beyond the interactions among the parts" – in the sense that taking into account the next higher level of organization to that under direct analysis is an intrinsic necessity specific to any approach that seeks to be considered emergentist (Feibleman 1954, 61; Campbell 1974, 180; Salthe 1985; Bergandi 1995; 2011; see also Jax 2006; Lefkaditou and Stamou 2006; Schizas and Stamou 2010).[7] According to theoretical emergentism, the laws and theories of a level cannot be reduced to, or deduced from, the laws and theories of a less complex level of organization. This will be true from the point of view of both the developmental and evolutionary processes.

Several of the many authors who have played an important role in elaborating hierarchical perspectives in the evolutionary and developmental domain merit particular mention. David Sloan Wilson elaborated the post Wynne-Edwardsian version of group selection; the trio of paleontologists, Eldredge, Gould (1972) and Vrba (1984), instead supported species selection; and finally, Oyama (1985) supported the need to strictly correlate developmental and evolutionary studies.

Wilson, in the wake of the process of population sub-division begun by Wright, introduces a new concept of group, the "trait group," which is a smaller sub-division of demes. These trait groups are found very frequently in nature and concern the interactions that take place before and after the dispersion phase. However, like the Chicago school of animal ecology (Allee 1931, 361-362; Allee, Park, Emerson, Park and Schmidt 1949; Wynne-Edwards 1991; Blomquist 2007), Wilson considers that the process of natural selection is constituted by two components: that of individual selection *and* that of group selection. But his specific model considers that the first component operates on the fitness of individuals within small, isolated, local populations, the trait groups. Group selection, instead, operates on the differential productivity of local populations within a global population (Wilson 1980, 45; 1983, 174-175). This multilevel selection theory, the legitimate pluralism of Wilson and Sober, involves the acknowledgement that various levels of biological organization can

[7] Methodologically speaking, this position largely overcomes the "pragmatic holism" proposed by Simon (1981), and it converges substantially with the weak form of antireductionist methodological emergentism supported by Schaffner (1993, 411-414; 2006, 382-383).

operate as units of selection – from genes to groups, and including individuals – with each level being characterized by specific adaptations (Wilson 1997, 2; Sober and Wilson 1998, 98-100, 329-332; Okasha 2006).

Wilson's version of group selection is an epistemological hybrid that, from an ontological viewpoint, reveals itself to be an interesting proposition. Through selfish evolutionary processes arise superorganismic, functionally organized, emergent entities – biotic communities. However, from a methodological point of view the concept of the emergent properties of a whole (totality, entity, individual) implies that they cannot be predicted, or deduced, from the study of the characteristics of its components or from the study of the interactions among its components. In other words, a strictly analytical additive approach is methodologically unsuited to the aim of understanding the emergent properties of an entity:[8] Wilson clearly identifies supeorganismic entities as characterized by emergent properties (Wilson 1980, 2). Therefore, the analytical approach that structures the analysis of the processes that are explained by the theories of individual and group selection (e.g. Wilson 1983) turns out to be neither applicable nor functional. Indeed, if the analytical approach is revealed to be heuristically useful, this directly shows that the superorganismic entities (biotic communities) are not ontologically emergent entities. The two possibilities cannot coexist in the same research programme, since they are logically contradictory.

The problem of selection units is not limited to considering only the genic, organismic, and populational levels, but also involves the species level. Speciation is at the center of macro-evolutionary processes. The focused attention on these processes has been accompanied by an openly critical position regarding the theoretical paradigm that emerged through the modern synthesis of evolution, which considers change in frequencies within a population as the building block of evolutionary processes (Stanley 1975, 650; Gould 1980, 119; Arnold and Fristrup 1982, 117). Initially, particular importance was attributed to the highly homeostatic systems that take part in genetic reorganization during the speciation process (Eldredge and Gould 1972; Gould and Eldredge 1977). A hierarchical and emergentist theory of evolution has gradually been built. Selection, acting on the variation of emergent characters (heritable and interacting with the environment), would produce differences in the birth and death rates of the various individual entities (gene, organism, population, species). Species selection will take place in the interaction between the heritable

[8] On the limits of decomposition and aggregative approaches and the role played by extra-systemic context-sensitivity in the determination of system properties, see Wimsatt (2007, 274-312).

emergent characteristics and the environment. Some examples of these characteristics would include the spatial and genetic separation among populations (Vrba and Gould 1986, 218-219).

Furthermore, with regard to the selection of species, it is important to note that Vrba and Eldredge, in their quest to expand the attribution of emergent properties to the species level, came up against a greater epistemological incoherence. Indeed, they consider that, "[t]he term 'emergent' does not imply necessary irreducibility, or unpredictability from observations at lower levels. […] we may understand precisely how a particular protein is produced by the genetic material but still recognize that that protein first entered at the phenotype level and is not the simple sum of genic characters" (Vrba and Eldredge 1984, 153; cf. Vrba 1984, 324). They therefore reserve themselves the right to continue to deem "emergent" characters that can be understood by referring exclusively to lower levels of organization. In this way, paradoxically, they deny the more peculiar aspect of the notion of "emergence," even while retaining the aspect of "novelty" that it implies.

For a long time, Gould shared the idea that emergent characters are the best indicator of the existence of macroevolutionary processes at the species level (Vrba and Gould 1986, 218). In later papers, he considered this criterion too restrictive (Gould and Lloyd 1999, 11907-11909; Gould 2002, 656-666). To remain valid, in order to identify "unambiguous cases for species selection" (Gould 2002, 658), the criteria needed to be expanded to take into consideration "exaptations," those non-emergent characters that contribute to species fitness (Gould 2002, 662). Gould thus dropped the emergent character approach – implying the necessary corollary of the existence of downward causation – and preferred what he designated as emergent fitness, or the interactor approach. He maintained: "I strongly advocate that we define higher-level selection as the differential proliferation of relevant evolutionary individuals based on causal interaction of their properties with surrounding environments – rather than by representing the effect of higher-level membership on the fitness of a designated lower-level individual" (Gould 2002, 656). In this way Gould bought into Hull's interactor definition (Gould 2002, 613- 616). He considered the species as the reference individual of the macroevolutionary process, and also restricted the importance of emergence in the identification of such processes. However, in so doing Gould ran into a logical inconsistency concerning the overall picture of his theory, for three reasons.

In the first phases of development of Gould's critical analysis of the reductionist approach, which founded population genetics and the modern synthesis of evolution, the leading goals were the affirmation of the ontological reality of macroevolutionary processes, and therefore of the necessary existence of paleontology as a reference discipline for such processes. Gould believed that it was not sufficient to extrapolate the results obtained from population genetics to other organizational levels, and made clear and repeated references to the notion of emergence. Thus, in his critical review of Darwinian and neo-Darwinian natural selection, emergence plays a central structural role and not a peripheral one. In the last phase of development of Gould's thought, emergence stops being the focal point of his theoretical position, thereby weakening his overall theoretical view. In fact, the *raison d'être* of macro-evolutionary theories lies in the idea that the different organizational levels that take part in the evolutionary processes are differentiated because of the specific emergent characters that distinguish them. Once it has been accepted that this is the founding premise of such theories, we cannot, without risking a sort of epistemological misdirection, marginalize the significance of the concept of emergence.

Secondly, the introduction of Hull's concept of individuals does not have to be understood as giving possible or immediate support to an emergentist view of the evolutionary process. From a formal point of view Hull's epistemological position, with its reference to entities as "cohesive wholes," can be confused with an emergentist one. Nevertheless, a closer examination of this position reveals its fundamental neutrality or, still better, its flexibility, with regard to the choices of the reductionist and emergentist camps, at least from a methodological point of view. In this respect, certainly, Hull considers the species as an individual, an organized entity, in a similar way to an organism (Hull 1976, 181). His perspective undoubtedly has an organicist accent.[9] However, Hull never refers to emergent properties, but rather to the existence of the cohesion of the internal organization of the entity in question, to spatio-temporal limits comparable to those of the other entities on which selection acts. While, like Lewontin (1970), Hull holds that selection operates at various organizational levels, as has already been pointed out, he nevertheless considers that the fitness of populations is understandable as the sum of individual fitnesses, and therefore explicable essentially in terms of the next lower level of organization. In other words, he considers populations as "structural wholes," and clearly denies the existence of emergent properties at this level of biological organization.

Therefore, even though Hull seems to appreciate the importance of the totality concept, which is so influential in the holistic and emergentist perspectives, his

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[9] Concerning species considered as classes of members and not individuals space-temporally defined as organisms, see Ruse (1998, 286-287).

methodological and epistemological field of reference, at least in the case of group selection, is reductionism, and not emergentism. I can suppose that the integration of Hull's concept of individuals into Gould's theoretical framework is not totally unrelated to the latter's marginalization of the emergence concept, which he had previously treated as a priority. Yet if we want to ensure the stability of the entire theoretical hierarchical framework built up around macroevolutionary phenomena, the focal importance of the concept of emergence and of emergentist methodology must be emphatically maintained. In this respect, from an epistemological point of view, it could prove more functional to use a transactional perspective rather than an interactional one, since the transactor connotation focuses on the emergence concept and on the internal correlation among different organizational levels. Moreover, this perspective will necessarily bring into focus the supposed emergent specificities of the higher levels of biological organization that play a role in evolutionary processes.

By affirming that only one of the necessary aspects for the existence of an emergentist perspective needs to be taken into account,[10] Gould weakens his position and exposes his macroevolutionary view to the risk of being co-opted by a traditionally microevolutionary reductionist methodology. In fact, since he denies the effect of the higher level of organization, or at least ceases to treat it as a priority in defining the focal level of analysis, there is no longer any reason to consider the classic analytical method inadequate. Downward causation – methodologically understood as taking into account both the primary level of analysis and the adjacent levels – must be considered as the *sine qua non* of methodological emergentism. Otherwise emergentism would be limited to a simple ontological position, an act of faith about the nature of reality, with no repercussions on concrete methods. This would obviously weaken the heuristic capacity of emergentism and amount to an implicit acceptance of the analytical approach as the sole possible methodology. In Gould's subsequent effort to make his model more testable and general, he marginalizes the significance of emergent characters in the identification of species selection, but by dropping the only element that methodologically distinguishes emergentism (downward causation) from reductionist methodology, he tends to undermine the explanatory potentialities and applicability of the hierarchical view of the evolutionary process.

Finally, Oyama's position concerning the strict correlation between developmental

[10] The interactions existing between the entity and the surrounding environment, interactions that produce a differential proliferation of individuals.

and evolutionary studies is grounded in the refusal of the informational gene concept, according to which genes intrinsically contain programs, plans with a predetermined formative power generating specific organism traits (Oyama 2000a; 2000b). These traits would be "filtered" only in a second instance by the environment, the latter being only a passive support and not a causal partner in development and evolution. More particularly, Oyama points out that the "genetic imperialism" dominant in developmental and evolutionary studies involves the asymmetric dichotomy between the causal values of genes and the environment (Oyama 2000b, 67-68, 107, 197-198).[11] The implicit solution is that even if some phenotypic traits are genetically determined and others environmentally determined, in the determination of most phenotypic traits causal preeminence is attributed to the genes. To the contrary, she maintains that the intricacy of the multi-layered developmental and evolutionary processes renders it possible to focus attention only on genetically or environmentally determined variation, but not on genetically or environmentally determined traits.

At the core of Oyama's conception lies her rejection of genes considered as prime movers, which means a refusal of the Dawkinsian self-actional, gene-centered perspective of biological processes. Moreover, a typical transactional accent can be found in Oyama's view when she argues that, for example: "[…] a gene initiates a sequence of events only if one chooses to begin analysis at that point" (Oyama 2000a, 40, 206). The transactional dimension of the organism-environment complex renders impossible any attempt to argue that in phylogeny and ontogeny the genes represent the primary causal factors. Genes cease to be the unmoved movers, the *deus ex machina* solving the evolutionary puzzle, since the embeddedness of ecological and developmental system relationships makes any identification of ontologically separate, independent elements, which are also causally relevant, a meaningless abstraction. This position must not be confused with a naive, vague holistic view, since the value differentiation between various interactants persists, but at the same time the equivalent potential causal relevance of the different factors in the developmental and evolutionary processes is affirmed.

Oyama considers that the interactional perspective structuring the biological and psychological studies has failed (Oyama 2000b, 47; see also Oyama, Griffiths and Gray 2001, 4-5). To avert the ambiguities present in the interactional worldview, she proposed a constructivist interaction worldview of these processes. Unfortunately, even if this elucidates

[11] On this specific point, Sarkar is in agreement with Oyama when he explicitly recognizes that an organism is the result of the history of the interactions between its genotype and its environment (1998, 177).

the active, permanent interpenetration and interchanging construction characterizing the multilevel reality of developmental and evolutionary processes, it does not escape the semantic and epistemological repercussions of the term 'interaction.' To allow clarification of the semantic and operational categories present in the debate, it is helpful to recognize the epistemological usefulness of the differentiation between self-action, interaction, and transaction proposed by Dewey and Bentley. This differentiation permits us to clearly understand that the interactionist point of view is not a failed holistic conception. Rather, in reality, it is totally coherent with a dualistic conception of the entities at issue, which are in more extreme cases considered as separate, fixed, and having external, and not internal, mutually constructive relationships.

Conclusion

Sometimes scientists and philosophers conceive of evolutionary processes in transactional, systemic, holistic terms, but they express themselves and model these processes in interactional terms. A transactional perspective, consciously recognized, can play an important role as an epistemological framework for scientific and philosophical positions that oppose a reductionistic, self-actional, and gene-centered view of evolution and development. Such a perspective would also help to avert the semantic and methodological ambiguities arising from the interactional worldview.

In the disciplines of evolutionary biology and ecology, proposals of the replicator and interactor concepts have been able to focus attention on the eventual self-actional and interactional aspects of evolution. The introduction of the transactor concept is intended to propose an epistemological tool that can be used to take into consideration the eventual emergent characteristics of evolutionary processes, particularly at higher organizational levels. Until now, the interactor played a supporting role for all those who would propose a non-reductionistic, non-gene-centric perspective of the evolutionary process. In reality, the interactional point of view cannot hide certain inconsistencies concerning the methodological dimension, in particular unconditional acceptance of methodological reductionism. This is in direct opposition to the concept of emergence, which structures perspectives that want to be non-reductionistic and more focused on the influence of higher organizational levels on evolutionary processes. More specifically, the transactor must be understood as a methodological construct that implies that: (a) the existence of specific emergent properties may express specific adaptations; (b) in the search for the causal explanation of adaptations, we can avoid resorting to the analytic decomposition of the bottom-transactors; and finally, (c) the need to take into consideration the upper transactor is revealed when the differential frequency of the proliferation of an entity (gene, organism, deme, population, species) is sensitive to, or depends on, its "context". In other words, the fitness of such entities can depend on specific selective-environmental factors and on the influence of the higher transactor, at least as much as on the specific properties of the entities in question.

Finally, the clear difference between the approach based on the "interactor" and the proposed approach based on the "transactor" lies in the consideration that, in the latter, the ecological and selective environments are integral aspects of the identification and definition of the entity on which selection operates. The transactional perspective permits outlining a different imaginative scenery in which there is an ongoing mutual, reciprocal relationship between the environment and the entity under selection, whereas from an interactional point of view these are viewed as in a causal relationship, but as definitely separate. This separation ordinarily confers preeminence on the inward biological factors over the environmental ones.

In other words, I suggest that if we accept a transactional ontological and epistemological perspective, the entity upon which the selection works, and its environment, which in an interactional (and self-actional) perspective are considered as separate entities, will cease to be considered as such. In this case, the pervasive, co-determinant, dialectical integration between these aspects of the evolutionary processes becomes the epistemological core that is able to redefine scientific models so as to elicit more careful interest in the eventual emergentist dimensions of these processes. A direct and fundamental consequence of this worldview is that, until proved otherwise, *a priori* every transactor, or transactional level, legitimately has a possible causal role in the determination of the adaptations and other evolutionary processes that can be generated in the whole range of biological organizational levels.

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