Position paper

Universal symbiogenesis: An alternative to universal selectionist accounts of evolution

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Abstract

The process of symbiogenesis need not be confined to either the microcosm or the origin of eukaryotic beings. On the contrary, just as natural selection today is being universalized by evolutionary biologists and evolutionary epistemologists, symbiogenesis can be universalized as well. It will be argued that in its universalized form, symbiogenesis can provide: (1) a general tool to examine various forms of interaction between different biological organisms (regular symbiogenesis, hybridization, virus-host interactions), and (2) new metaphors for extra-biological fields such as cosmology, the cultural sciences, and language. Universal symbiogenesis can thus complement universal selectionist accounts of evolution.

Keywords: Universal symbiogenesis, universal selectionism, evolutionary epistemology, culture, origin of life, hybridization, viruses

1. Introduction

The time that natural selection and evolution were synonymous concepts is long gone. Today, we know that life's evolution takes on many forms and natural selection is one amongst many theories that tries to capture parts of the evolutionary process. Other theories that explain parts of life's evolution are symbiogenesis, neutral theory, punctuated equilibrium, hybridization, systems theory, etc. (see for example Gontier, 2004; Ryan, 2006; Schwartz, 1999 for some overviews).

This paper deals with theoretical and philosophical issues of symbiogenesis (Margulis, 1999; Margulis and Sagan, 2000, 2002; Margulis and Dolan, 2002) and the role symbiogenesis can play in evolutionary theory. It will be argued that just as natural selection can be universalized from within an evolutionary epistemological position, symbiogenesis can also be universalized, providing an explanation for the origin of nucleated cells and cell organelles, together with other events that take place in the microcosm. More specifically, processes analogical to symbiogenesis can be distinguished within several layers of life and within the evolution of life's products (such as language and culture for instance). This universal process

of symbiogenesis can provide a complementary view to universal selectionism.

To make this view more comprehensible, I give a brief historical sketch of the origin of natural selection as a scientific theory. I explain how paradigm shifts and redefinitions of what exactly it is that natural selection tries to capture were introduced by neo-Darwinians and postneo-Darwinians. We shall see that it was these shifts that enabled the universalization of selectionism. Secondly, I propose a universal symbiogenetic scheme that can complement universal selectionism. Finally, I examine how universal symbiogenesis can be implemented as a logical approach for problem solving, with applications that include the study of viruses, hybridization, culture and language.

2. A Brief Historical Sketch on the Paradigm Shifts Concerning the Role of Natural Selection

Darwin and the introduction of natural selection

When the term "natural selection" was first introduced as an evolutionary mechanism by Charles Darwin (1857), it

was understood to (1) work passively and (2) external to the individual. The subtitle of Darwin's Origin of Species: the preservation of favoured races in the struggle for life already makes clear his ideas on natural selection. It is a theory that explains how adaptive organisms are preserved. Organisms live in competition with each other because environmental resources are often scarce (the so-called "struggle for existence"). Organisms also vary physically (variation), and because of this anatomical variation, some organisms are able to obtain resources better than others. The former are naturally preserved (or selected) by the environment in which they live and are called adaptive organisms. Adaptive organisms have a greater chance of living long enough to be able to reproduce and pass on their adaptive traits to their children. Maladaptive organisms, on the contrary, struggle to survive in a certain environment and are thus less likely to reproduce than the adaptive ones.

The difference between adaptation and fitness is that adaptation means being able to cope in a certain environment, while fitness concerns the number of offspring an adaptive organism is able to produce. Thus fitness becomes a measure for adaptation.

The main point that Darwin was making is that evolution by means of natural selection occurs at the intersection between a living organism (that has its hereditable variation) and the environment. As eminent scholars such as Lewontin (2000) have pointed out before me, this implies that natural selection occurs external to the individual. It is the phenotype or visible organism, not the genotype, that is the unit of selection. And selection also works passively: the elimination of the unfit organisms occurs directly (since they cannot survive in a certain environment), while the preservation of the fit occurs indirectly. That is, according to Darwin, natural selection cannot cause the adaptive traits to evolve, but it can enable the preservation of these traits through natural selection, once they have evolved.

The neo-Darwinians and the problem of the origin of variation

Darwin did not know how variation occurred or how it was transmitted faithfully from one generation to the next but he was sure that natural selection was not the mechanism that explained the origin of variation. On the contrary, he often used Lamarck's theory of use and disuse and his own theory of gemulles to address this problem (for an excellent overview on this matter, see Schwartz, 1999).

The problem of how variation occurred was solved by the population geneticists that combined Mendelian hereditary laws (that explain the passing on of existing variation) with de Vries' mutation theory (that explains the introduction of novel variation through mutations). And these ideas in turn became combined with Darwin's mechanism of natural selection. With the foundation of the

Modern Synthesis in the 1930s (see Gontier, 2004), selection operating on random mutations becomes the core concept in explaining evolution. Since then, the focus for scholars interested in evolution would lie on two processes: the formation of the sex cells, where genetic mutations can possibly occur, and reproduction, where new variation is possibly transmitted vertically (Gontier, 2004: 280–281).

Furthermore, because of the population geneticists' rejection of Lamarckian inheritance, a strict distinction was made between ontogeny and phylogeny. It was argued that ontogenetic processes could not be used to explain phylogenetic events, a position that pioneering evolutionary embryologists such as de Beer and Goldschmitt had been supporting earlier (Schwartz, 1999). This distinction also contributed to the fact that natural selection was understood to be a process acting on a phenotype, instead of on the internal developmental features of an organism.

Post-neo-Darwinians and the role of natural selection

With the rise of post-neo-Darwinism, the concept of natural selection came to be investigated from other perspectives. Two main types of questions were raised. The first type of questioning concerned the workings or operation of natural selection. Examples of this type of query are: Is natural selection indeed something that only passively selects the fit through the elimination of the unfit? Can natural selection also cause adaptive variation? The second type of questioning concerns the applicability of natural selection as a mechanism to explain the evolution of different phenomena of life which relates to the units and levels of selection debate. Examples of this type of query are: Does natural selection also select units other than the phenotype? Is the environment the only level where selection occurs?

The operation of natural selection and the applicability of natural selection

The concept units of selection was first introduced by Lewontin (1971) in a homonymous article to counter Hamilton's idea that groups rather than a phenotype could serve as a unit of selection. The concept levels of selection in turn was introduced by Brandon (1982). The units and levels of selection debate investigates in which domains natural selection, as a mechanism, is applicable. And the applicability of natural selection as a mechanism in turn raises questions concerning the operation of natural selection. More specifically, in his seminal article, Lewontin (1970: 1) investigates how exactly it is that natural selection operates. He argues that "... a logical skeleton ... " can be drawn from natural selection that takes on the following formula: "... phenotypic variation, differential fitness and heritability of that fitness". This formula can be applied to "... different units of Mendelian,

cytoplasmic, or cultural inheritance". In other words, according to Lewontin, this skeleton (1) explains the operation of natural selection and (2) it helps investigate where the mechanism of natural selection can be applied. Lewontin concludes that it can be applied in both biological and cultural domains.

Most of the questions raised by post-neo-Darwinians concerning the operation of natural selection however can be traced back to a single neo-Darwinian, the population geneticist Ronald Fisher (1931). In 1931, Fisher introduced the Dominance Theory, according to which the wild type is the "... unsuccessful successor ..." (Schwartz, 1999: 247-253). That is, although the wild type (the dominant phenotype) is well-adapted to the environment, for evolution by natural selection to occur, it must be replaced by still better adapted individuals who are able to produce even more offspring than the wild type. It is assumed that natural selection weeds out maladaptive organisms and thus is indirectly responsible for the survival of the adaptive ones, and, at the same time that it can also directly work upon the adaptive organisms and thus actively direct evolution.

In this respect, two post-Neo-Darwinian scholars, Dawkins (1976) and Eigen (1996), should be mentioned who were especially inspired by Fisher's ideas. Dawkins assumes that natural selection does not merely eliminate the unfit, but actually explains the origin of adaptive traits. Furthermore, Dawkins restricts the working range of the concept of natural selection to the gene and genotype rather than the phenotype, and in so doing he *internalizes* natural selection (Gontier, 2006a). This internalization of selection entails that it is no longer the phenotype that is selected at the level of the environment. Rather, the complete genotype, of which most of the genes are not expressed phenotypically, is understood to be the unit of selection.

Furthermore, Dawkins takes the discussion one step further, when he introduces the concept of a replicator and, in 1983, the idea of *Universal Darwinism* in a homonymous article. According to Dawkins (1982: 162), a replicator is "... any entity in the universe of which copies are made". Genes, but also memes are understood to be such replicators, while these replicators become the unit of natural selection.

With the concept of Universal Darwinism Dawkins argues that if life were to originate anywhere in the universe, and if life would portray adaptive complexity, it can only have evolved by natural selection. The opening paragraph of his *Universal Darwinism* paper goes as follows:

"It is widely believed on statistical grounds that life has arisen many times all around the universe However varied in detail alien forms of life may be, there will probably be certain principles that are fundamental to all life, everywhere. I suggest that prominent among these will be the principles of Darwinism. Darwin's theory of

evolution by natural selection is more than a local theory to account for the existence and form of life on Earth. It is probably the only theory that can adequately account for the phenomena that we associate with life." (Dawkins, my emphasis, 1983: 15).

Thus according to Dawkins, natural selection is not merely one of the theories that can explain the evolution of life here or anywhere else in the universe, it is probably the only theory. And in its universalized form, replicators and vehicles can be distinguished not merely within the evolution of life, but also for example within the evolution of culture. The latter implies that different units and levels of universal Darwinism can be distinguished.

Eigen was also inspired by Fisher's Dominance Theory. According to Eigen, it is not the wild type¹ that drives evolution (that is the unsuccessful successor) but the quasispecies (the mutations of the wild type²) that are the target of selection.

"In this way, the average of all sequences is identical with the individual sequence of the wild type, even if the latter is present in vanishingly small amounts or not at al. Such a distribution we call a quasi-species. It is the target of selection." (Eigen and Schuster, my emphasis, 1977: 20)

With the introduction of the quasi-species, again the emphasis is put on replicators (in Eigen's view, RNA- and DNA-molecules, viruses and bacteria). Furthermore, Eigen too universalizes natural selection, albeit in a different way than Dawkins, since he turns natural selection into a physical law that, according to him, is *only* applicable to these replicators. It is argued that natural selection literally "directs" these replicators in their evolution:

"This directedness of the evolution process is perhaps the clearest expression of the present-day paradigmatic change in the established Darwinian world-picture. Anyone who is accustomed to base his world-view dogmatically upon Darwin, calling himself a Darwinist, will be reluctant to accept this new interpretation. ... However, our argument is a physical one, so that two assertions must be logically (in the end mathematically) deducible, and the consequences of a theory must differ from those of other models, with differences that are experimentally testable. ... [O]ur interpretation says simply: If selection results from differing efficiencies of reproduction, then this occurs in the sense of the quasi-species model and not in the way envisaged by the classical wild-type model. If evolution

¹ It must be emphasized that, according to Fischer, the wild type was an existing entity, that roughly parallels our notion of the dominant phenotype. Today, however, mostly because of Eigen's work, the wild type is understood to be a statistical, non-existing entity.

² "A quasi-species is defined as a given distribution of macromolecular species with closely interrelated sequences, dominated by one or several (degenerate) master copies." (Eigen and Schuster, 1977: 541).

occurs on the basis of natural selection, then it is value-oriented" (Eigen, 1996: 29).

According to Eigen, natural selection can play an active role in evolution as well since it is value-oriented, which means that natural selection will and can only select more adaptive successors than the wild type. It is only when the quasi-species are more adaptive than the wild type that the former can replace (dominate) the latter.

Vertical evolution, speciation and the pace of evolution

Natural selection, either in its original or universalized form, explains evolution to be a process of splitting and branching where evolution evolves from the simple to the complex and from single to many. This point brings us to another process that population geneticists wanted to understand that was not explained by Darwin, namely the problem of speciation. If for example, evolution by means of natural selection implies the replacement of the wild type by better adapted, mutated copies of that wild type, then the existence of different species becomes problematic (the replacement-part would entail that only one species would be extant) (see Gontier, 2004). Therefore, Mayr (1997) for example would introduce the concept of allopatric speciation by peripheric isolation.

In general, because of the results of Dobzhansky's and Morgan's fruit fly experiments, population geneticists would argue that micro-evolution serves as a template for macro-evolution (Schwarz, 1999: 284-92). specifically, since mutations are what causes novelty, and mutations are deviant forms of the master copy, evolution can only occur by means of splitting and differentiating from the original copy. They argued that the small random mutations that cause this individual variation ultimately also lies at the basis of speciation, since speciation is caused by the accumulation of these small mutations. At the macro-level, speciation occurs when a group of individuals (because of isolation and the occurrence of genetic mutations within this isolated group) would deviate that much from the original species that sexual reproduction between the two becomes impossible.

Since it is assumed that micro-evolution results in macro-evolution, evolution must occur slowly, thereby producing a long sequence of intermediates. Furthermore, because both micro- and macro-evolution imply the deviation of an existing structure, evolution occurs through splitting and differentiation, rather than through mergings. When individuals are able to reproduce fertile offspring, they are understood to belong to a single species and when they cannot reproduce fertile offspring, they are understood to belong to different species. Hence, the possibility to cross different lineages becomes the criterion used to assign individuals to one species and, conversely, the impossibility to cross different genealogical lineages becomes the sole criterion for speciation. In a real sense therefore, symbiosis

and speciation are mutually exclusive principles³. We return to this topic later.

Summary: The different paradigm shifts concerning the role of natural selection

On a meta-level, the following paradigm shifts concerning the role of natural selection have occurred within the history of evolutionary biology. Darwin himself argued that natural selection was the mechanism that eliminated the unfit, and allowed for the preservation of the adaptive organisms; the latter were selected naturally. Natural selection however had only the role of eliminating the unfit: it was not the cause of (novel) variation. Neo-Darwinians (alternatively known as the populationgeneticists) synthesized Darwin's idea of evolution by means of natural selection with Mendelian heredity laws that explain variation and de Vries' mutation theory that explains the introduction of novel variation. These authors too argued that especially the introduction of novel variation cannot be explained by natural selection, since natural selection does not cause genes to mutate. Rather, mutations are stochastic events, that, once evolved, can become the subject of selection (for a full elaboration of these views, see Gontier, 2004). Therefore, Morgan for example could argue that selection differs from evolution since selection: " ... has not produced anything new, but only more of certain kinds of individuals.' ... 'selvolution ... means producing more new things, not more of what already exists. '(cited in Schwartz, 1999: 241)

That mutations are stochastic events even today is still a view that is widely subscribed to. But since Eigen's seminal work on the quasi-species, it is argued that the selection of mutations that are better adapted than the wild type does not occur in as "blind" a fashion as the neo-Darwinians

³ There are of course numerous species concepts (see for example Mallet, 2006 for an recent overview) available, besides the biological species concept that was first introduced by Mayr (1996), but this species concept remains the dominant concept used in current evolutionary biology. "Zoologists, those who professionally study animals, have imposed a distinct concept of species, which they call the 'biological species concept'. Coyotes and dogs in nature do not mate to produce fully fertile offspring. They are 'reproductively isolated'. The zoological definition of species refers to organisms that can hybridize – that can mate and produce fertile offspring. Thus organisms that interbreed (like people, or like bulls and cows) belong to the same species. Botanists, who study plants, also find this definition useful." (Margulis and Sagen 2002: 4–5).

⁴ Mendel's laws do not explain the introduction of new variation either, a point also emphasized by Margulis (1999: 26–27): "Red male and white female flowers produced seeds that grew into pink offspring. But the flowers generated by pink parents were just as red or just as white as their grandparents had been. [...] Mendel's factors were correlated with the inheritance of unchanged characters."

assumed. Rather, the superior mutants are selected by necessity:

"There is an essential difference between the ideas expressed here and the neo-Darwinian idea of an alternation between mutation (=chance) and deterministic selection of the superior mutant (=necessity)" (Eigen, 1996: 27).

Thus Eigen's quasi-species model demonstrates how natural selection can direct evolution towards better adapted organisms, instead of merely eliminating the unfit and preserving the fit. But Eigen argues that natural selection as a physical law is exclusively applicable to replicators, and not to multi-cellular organisms for example. Eigen (1996: 39): "... there is no 'universal formula' that could be used to deduce rigorously the origin of life and to explain its miraculous variety, from the simplest virus to the human mind" (Eigen, 1996: 39).

Dawkins, on the contrary, does endorse the view that natural selection can be universalized to account for life's evolution on this planet and elsewhere in the universe and it can also be applied to extra-biological fields such as cultural evolution. Furthermore, Dawkins (1976, 1982, 1983), moves away from the selection of an external phenotype to the selection of an internal genotype and thus natural selection no longer works external to the organism: no longer is a phenotype selected at the level of the environment through the process of natural selection. Rather the gene(s) or replicator(s) become(s) the unit of selection and the organism is understood to be a mere vehicle that is not the unit of selection. And the replicator as a universal unit of selection is selected at different levels.

Hence, following Dawkins, natural selection becomes a theory applicable in biological and extra-biological fields alike. This investigation of the operation of natural selection also triggered the units and levels of selection debate which asks about the different applications of this mechanism. In a real sense, it was the population geneticist's idea that micro-evolution also explains macro-evolution that set in motion the avalanche of post-neo-Darwinian theories concerning the units and levels of selection debate. Finally, these innovations also lead to the idea that evolution by means of natural selection is solely a matter of branching and splitting.

3. Evolutionary Epistemology and Universal Selectionism

The philosophy of science, more specifically the philosophy of evolutionary biology and also psychology have undergone similar paradigm shifts throughout their historical development.

In philosophy, W.V. Quine (1969) was one of the first scholars to argue that natural selection could not only explain the evolution of life, but also the evolution of human cognition. Thus, according to Quine, natural

selection as a theory could be used to study, what were at that time believed to be extra-biological topics, such as philosophical problems concerning the reliability of our cognitive apparatus.

As already argued, in 1970 Lewontin abstracted a logical skeleton of natural selection that could be applied to biological and cultural evolutionary phenomena. The idea of abstracting such a skeleton from natural selection was however not an idea that originated within biology, but rather in psychology. As early as the 1950s, the psychologist Donald T. Campbell (1959) abstracted a formula from natural selection called blind variation and selective survival, which he would later adjust to blind variation and selective retention (Campbell, 1972). He applied this formula especially to study the growth of knowledge and the evolution of cognition mechanisms (e.g. science, culture or language but also for example echolocation was conceived as a knowledge mechanism) for all living organisms from within a comparative psychological approach. Furthermore, Campbell was convinced that his formula could be applied to other domains as well and thus that his formula was a universal one. Campbell called this approach evolutionary epistemology (EE)3.

Since then, numerous selectionist formulas have been developed. There is for example the *generate-test-regenerate scheme* developed by Plotkin (1995), and the *replication-variation-environmental interaction*⁶ scheme, coined by Hull (1980, 1981, 1988). For a discussion of all these different formulas see Cziko (1995) or Gontier (2006c).

Depending on the evolutionary epistemological theory involved, it is argued that these universal selection formulas can serve as a heuristic or a template to model the evolution of a wide spectrum of phenomena, e.g. immunological processes, the evolution of the brain (also called neural Darwinism, cf. Changeaux, 1985), knowledge, learning, culture, etc. The application of natural selection to so many different biological and extra-biological domains immediately brings into focus new questions concerning units and levels of selection. Thus the units and levels of selection debate today is also one of the major research topics within evolutionary epistemology.

Turning specifically to the problem of cognition and knowledge once more, according to the Stanford Encyclopaedia of Philosophy, EE is defined as: "... a

⁵ A full overview of evolutionary epistemology is beyond the scope of this article since there are numerous different theories within the field (but see Bradie, 1986; Callebaut and Pinxten, 1987; Callebaut, 1993; Gontier, 2006a, 2006c; Wuketits, 1990).

⁶ David Hull (1980, 1981, 1988) again countered Dawkins' universal concept of a *replicator* with his universal notion of an *interactor* that was to be understood as the proper unit of selection, and which largely corresponds to the classical idea that the phenotype is the unit of selection that is selected at the level of the environment.

naturalistic approach to epistemology, which emphasizes the importance of natural selection in two primary roles. In the first role, selection is the generator and maintainer of the reliability of our senses and cognitive mechanisms, as well as the "fit" between those mechanisms and the world. In the second role, trial and error learning and the evolution of scientific theories are construed as selection processes" (Bradie and Harms, 2004: 1).

Thus, according to this definition, EE focuses exclusively on natural selection and natural selection can (1) be understood not only as the maintainer but also the generator of the reliability of our senses and cognitive mechanisms. This is because adaptation results in a fit between these senses and cognitive mechanisms and the outer world. (2) Natural selection can also serve as a heuristic metaphor to explain trial and error learning and the evolution of scientific theories. And here too a shift has taken place that runs parallel with the transition from neo-Darwinians to post-neo-Darwinians. For example, Donald T. Campbell, the founder of EE, did not understand natural selection to be the generator, but the maintainer of our sense organs and cognitive mechanisms.

In sum, evolutionary epistemologists and evolutionary biologists, together, set in motion the idea that natural selection can be universalized to explain not only the evolution of animals, or life in general, but all kinds of evolutionary processes. One basic theme that unites all scholars working within EE is that all of life is the product of evolution. Therefore it is only logical to study the products of life from within an evolutionary framework as well. These products can include a wide range of phenomena such as cognition, knowledge, the brain, language and culture. Because these products are displayed by biological organisms, within EE it is thus argued that these products also require an explanation based on evolutionary theories. The goal of EE is therefore to develop general evolutionary schemes that can serve to explain these different evolutionary processes.

4. Problems with a Universal Selectionist Account

Universal selectionism, the only universal evolutionary theory?

Universalizing natural selection has turned out to be a fruitful endeavour since it allowed for a more systemic and analytical approach to various evolutionary phenomena. A great deal of progress has been recorded in many fields since they endorsed a universal selectionist approach.

The problem with universal selectionist accounts today is that, because of its success, natural selection is understood to be not only necessary, but also sufficient to explain *all* of life's phenomena. Hence the universalization of selection becomes an end in itself, rather than a means to

capture certain aspects of life's evolution. This unfortunately also leads to the neglect of other evolutionary theories that encapsulate different or the same evolutionary phenomena.

If we look at Cziko for example, he boldly argues (using Dawkins' ideas) that universal selectionism alone is valid: "Let us recall that Dawkins' conclusion is based on the argument that the process of cumulative blind variation and selection is the only currently available scientific explanation that is in principle capable of explaining the emergence of the adapted complexity required for life" (Emphasis is mine, Cziko, 2005: 303).

In his book, Without Miracles, Cziko does not add anything new to the ongoing selectionist debate, rather he basically summarizes all claims on universal Darwinism made by Dawkins, Changeaux etc. and classifies them under the vernacular universal selectionism. In chapter 16 of his book, he argues that concerning natural selection: "Although it may be far from perfect, no other general-purpose construct-and-search procedure has yet shown itself to be as capable for such broad range of problems, and none other is able to explain the remarkable achievements of fit we continually encounter in both natural and human-made environments" (Emphasis is mine, Cziko, 1995: 314).

The reason that "... no other general-purpose construct-and-search procedure ..." has challenged natural selection is that no other such general formula has been constructed yet. So far, only natural selection has been universalized. However, if we were to believe Cziko (315–326), no such universalization of other evolutionary theories would be necessary since "... punctuated equilibrium, direct mutation, exaptation, symbiosis and self-organization ..." are, according to Cziko (2005: 315), merely "... would-be challengers to natural selection".

Such bold claims cannot be justified without first examining what exactly it is that universal selectionism does and does not try to explain. After all, natural selection is only one of many evolutionary theories that explain and describe certain aspects of life's evolution. Secondly, we need to investigate whether or not it is possible to universalize evolutionary theories other than natural selection and thirdly, these different universal theories then need to be compared with universal selectionism. Only then will we be able to test Cziko's assumption that the other evolutionary theories are merely would-be challengers to natural selection.

What does universal selectionism explain?

To begin with, from its conception by Darwin onwards, we have seen that natural selection explains adaptation. Furthermore, and as already pointed out earlier in this text, natural selection explains evolution exclusively by means of vertical transmission and hence it endorses linear speciation and branching models. Branching models of

life's evolutionary tree are useful. However, if we understand universal selectionism to be the only theory available to explain certain evolutionary phenomena, we run the risk that non-vertical transmission models are not only neglected, but even dismissed as unscientific. This is particularly true in the case of symbiogenetic studies but also in extra-biological fields such as anthropology or language origin studies, where this neglect becomes more and more a genuine problem. Let us focus for a moment on the field of language origin studies and draw some parallels with the evolution of life.

Biologists are not altogether aware that 19th century linguists were the first to introduce genetic branching trees into the realm of science. When faced with how different languages emerged, how they were related to each other, compete, and how they would go extinct, the linguists developed these trees to show the historical relatedness of different tongues. It was Haeckel, the first taxonomist, who introduced these models into evolutionary biology, a move also endorsed by Darwin (for a discussion see Hull, 2002; Richards, 2002). Thus, in this respect, linguistics and evolutionary biology share a common intellectual origin. For a while, the evolution of languages was even taken as evidence for the evolution of the human species and, fallaciously also of different human races. It is only natural that both fields are therefore faced with similar problems regarding their use of speciation models. Here three of such problems are briefly demonstrated.

- (1) Branching models assume vertical transmission of traits and therefore evolution is understood to be linear. On this view, older languages or older organisms are often mistakenly regarded to be less complex⁷. This view is wrongheaded in biology because: "Although eukaryotes are the most morphologically complex, microbes, the largest biomass in earth ..., have the greatest biochemical complexity" (Sapp, 2004: 1046). And also in linguistics, the idea that older languages are less complex is nowadays abandoned.
- (2) Because of the linearity built into the model, speciation models also exclude the possibility of a multiple origin of life. Rather it is assumed that life evolved from one Last Common Ancestor, and all languages arose from one proto-language. However, and I shall return to this point later in this article, much can be said in favour of a multiple origin of life (e.g. Dyson 1988). And although all spoken languages apparently descended from earlier languages, certain sign languages (e.g. the recently developed Nicaraguan Sign Language, Senghas, Senghas and Pyers, 2005) seem to develop out of home signs that have no prior affinity with spoken language.

(3) Branching models also a priori exclude the possibility that evolutionary lineages can merge. More specifically, branching models imply that speciation is the rule and mergings or horizontal crossings of lineages are the exception. Mergings of lineages however occur frequently through the processes of hybridization and symbiogenesis. And, more particularly, symbiogenetic processes involved in the merging of different prokaryotic organisms that would then evolve into eukaryotic organisms have demonstrated the following: that these crossings of lineages can also cause evolutionary novelty in life's evolution8. However, if it is assumed that the microevolution of genetic mutations (the mutations having vertically evolved from the master copy) are representative for macro-evolution, then cell-fusions will become neglected as possible sources for the introduction of evolutionary novelty9.

Also in linguistics, similar processes of lineage mixing can be distinguished. Language borrowing (the borrowing of certain words from other languages without transformation of the meaning of the word, e.g. the words tobacco, computer, ...) and language mixing (a process often witnessed in bilinguals where the lexicon of one language is structured by the grammar of another) all involve, to a greater or lesser degree, the merging of certain elements (see Croft, 2002 for an overview). In linguistics, these processes of language mixing and borrowing are studied by sociolinguists, which, as the name implies, work in a field of linguistics aligned, in part, with that of sociology. This sociological approach to different languages however is often contrasted to a selectionist, biological approach that focuses on the origin and evolution of the human capacity for language. So here too, splitting and merging become mutually exclusive concepts, although they need not be so a priori: aspects of language can split while others merge.

5. Universal Symbiogenesis

The above comparisons between language mixing and symbiogenesis are intriguing since both assume that horizontal mergings can cause novelty. Is it possible that symbiogenesis could be universalised in a way analogical to

⁷ Or, quite the opposite was assumed: that certain languages were degenerated forms of older, more complex languages (Frank, personal communication), comparable to the process of atavism that Darwin introduced.

⁸ It is important to note that after symbiogenetic processes have occurred, this newly evolved entity can again become the subject of selection, a point also made by Maynard Smith and Szathmáry (1995). However, the point of the above is that the initial merging is not the result of natural selection and the novelty that arises is not the result of random mutations.

⁹ "[...] symbiosis generates novelty." (Margulis, 1999: 12 and 8:) "Although Darwin entitled his magnum opus On the Origin of Species, the appearance of new species is scarcely even discussed in his book. Symbiosis ... is crucial to an understanding of evolutionary novelty and the origin of species. Indeed, I believe the idea of species itself requires symbiosis."

universal selectionism? And could universal symbiogenesis be applied to language evolution studies and elsewhere? This is the question we turn to for the remainder of this paper.

Dyson's symbiotic double origin theory of life

To my knowledge, Freeman Dyson (1988, 1998, 1999) was the first to universalize symbiogenesis. Dyson (1998) is a physicist who also has an interest in the origin of life and as such developed the double origin theory. Faced with the dichotomous views on life's origins where, on the one hand, it is assumed that life evolved spontaneously from protein-like structures and/or cells (e.g. Oparin, 1955; Fox and Dose, 1972); on the other hand, it is assumed that life got naturally selected in an RNA world (Eigen and Schuster, 1977; Eigen, 1996; Gilbert, 1986; Orgel, 1994), Dyson synthesizes both of these competing views. He argues that the autocatalytic molecule developed inside protein-like cells and was, therefore, the first parasite with which protein-like life ever had to deal with. Life thus did not originate once, the origin of life does not raise an either/or dilemma, on the contrary, it originated twice: once as metabolism and once as information, and both got combined symbiotically (Dyson, 1988: 81): "I am suggesting that the Oparin and Eigen theories make more sense if they are put together and interpreted as the two halves of a double-origin theory. In this case, Oparin and Eigen may both be right. Oparin is describing the first origin of life and Eigen the second."

Dyson was the first to import the principle of symbiogenesis to physics and chemical science where it can be applied at a molecular level, but he goes further than that. Whether regarding the origin of the universe, life or science, he basically distinguishes between two universally occurring phenomena: speciation events and symbiosis events. Both lie at the basis of order-disorder transitions, differentiation, and the emergence of new structures. All occur during rapid phases in history which are punctuated by long periods of stasis.

Dyson (1998:119) takes an evolutionary epistemological position when he states that: "The evolution of the universe and the evolution of science can be described in the same language as the evolution of life." Not only the origin of life or the origin of eukaryotic beings, but also symbiotic stars, galactic cannibalism or black holes can be understood as forms of symbiogenesis. He defines universal symbiogenesis as: "... The reattachment of two structures, after they have been detached from each other and have evolved along separate paths for a long time, so as to form a combined structure with behaviour not seen in the separate components" (Dyson, 1998: 121).

This definition, however useful for certain physical and biological phenomena, contains a few flaws. There is no

need whatsoever to assume *a priori* that there are only *two* structures that get attached *again*, as the term reattachment implies.

A logical skeleton of symbiogenesis

The above makes it clear that symbiogenesis does not only mark the evolution of eukaryotic beings, but also that it is a genuine evolutionary mechanism applicable to different phenomena. In the words of Carrapiço and Rodrigues (2005: 59060R-2): "... symbiogenesis should be understood as an evolutive mechanism and symbiosis as the vehicle, through which that mechanism unfolds."

The definition that Dyson proposes for universal symbiogenesis is biased towards his double-origin theory of life. In order to abstract a neutral universal scheme of symbiogenesis, let us examine what it is that is basic to symbiogenesis. What would a logical skeleton of symbiogenesis as an evolutionary mechanism consist of?

- (1) Symbiogenesis is all about *interaction*. Since we are looking for a universal formula, applicable to as many different phenomena as possible, it is better not to specify beforehand the type of interaction (mutualism, parasitism, symbiosis, commensalism), the type of entities that interact (individuals, lineages, traits, etc.) or the number of entities that interact. Specification would lead to exclusion and the goal here is to find as many possible types of symbiogenesis as possible.
- (2) Symbiogenesis also implies horizontal mergings that lead to permanent and irreversible changes, which form the basis of evolutionary novelty. Cyanobacteria that evolved into chloroplasts for example cannot return to their previous bacterial state; the process of symbiogenesis is thus permanent and irreversible. Once something emerged by symbiogenesis, it can (further) evolve vertically (through natural section). Important however, is the fact that the latter is always preceded by a horizontal merging of two or more different entities. The merging is permanent and irreversible, since the merged entities become fused in a single new entity with behaviour not seen in the prior existing separate components.
- (3) Such horizontal mergings can be fast, and are always discontinuous since the merging results in something new. A point also made by Zook (1998: 2): "By their associations, each results in a unique or novel metabolism and structure(s), both of which are not present prior to symbiosis".
- (4) Symbiogenesis is, as Margulis (1999: 43) already pointed out: "fi]ndividuality by incorporation", that is, a new distinctive entity emerges exactly because of the interaction.

This logical skeleton can be universalized into a heuristic formula as well, and I would suggest the following definition of universal symbiogenesis: Universal symbiogenesis is the process whereby new entities are

introduced because of the interactions between (different) previously independently existing entities. These interactions encompass horizontal mergings and the new entities that emerge because of this are called symbionts. The process is irreversible and discontinuous.

As stated, the definition is kept general to prevent as much exclusion as possible. The goal is to delineate different phenomena as symbiogenetic, including phenomena that were not previously thought to be of a symbiotic nature. Also, the well-used word *symbiont* is introduced here as a universal evolutionary epistemological concept that can complement Hull's *interactors* and Dawkins' *replicators*.

The symbiont in turn, once it evolved through non-selectionist horizontal merging, can become a unit of natural selection. This point is also made by Sapp (2004: 1047) when he defines the different types of biological symbionts under the all-encompassing notion of the *symbiome*: "... comprising chromosomal genes, organellar genes, viral genes, as well as other microbial symbionts, sometimes inside cells and always outside them, functioning across a continuum from parasitism to mutualism, depending on their nature and context. ... the symbiome must function as a unit of selection" (Sapp, 2004: 1047).

Applications of universal symbiogenesis

The question we now turn to is, given this universal schema of symbiogenesis, where can it be applied? What can be understood to be a symbiont rather than a replicator? These questions will be answered in the remainder of this article. Besides the obvious application of the universal scheme in micro-evolutionary symbiosis studies and the origin of eukaryotic beings, it will be argued that universal symbiogenesis can also include the study of viruses and their hosts, hybridization, and even extra-biological phenomena such as culture and language.

6. Universal Symbiogenesis and Viruses

Different authors (Gontier, 2006: 204–206; Roosinck, 2005; Ryan, 2002, 2004, 2006; Sapp, 2002; Villareal, 2004) have recently proposed that viruses should also be viewed from within a symbiogenetic perspective. Some viruses are able to copy their genetic material into the host genome and thus show a horizontal merging pattern due to a parasitic form of interaction between the virus and the host. Besides the penetration of the virus into the genomes of somatic cells, the germ cells are sometimes infected as well, resulting in the possibility of germ line transmission of the viral genome. This has considerable evolutionary potential. When somatic cells are infected, the result is an ontogenetically modified individual, while with germ line

transmission of the virus genome, the result might just be the formation of a whole new species.

According to this view and contrary to received wisdom, viruses should be regarded as living beings, at least from an evolutionary perspective (Ryan, personal communication) and as such they enter into a symbiogenetic union with their hosts. It is a very refreshing and promising idea to regard viruses as living beings that "... represent a major creative force in the evolution of the host ..." (Villareal, 2004: 296).

But even if one disagrees with this viewpoint, the universal symbiogenetic scheme presented above does not make any ontological statements about the nature of the entities that are involved in a symbiotic relation that can result into symbiogenesis. Thus, whether viruses are understood to be dead or alive, they can be entities that merge with other entities, an interaction that rapidly results in the formation of evolutionary novelty, as the universal symbiogenetic scheme implies.

Ryan builds on Villareal's (2004: 315) ideas of parasitic viral "... colonization..." and places these in a more symbiotic scheme that views "... viral infection of host germ cells as a widespread but little-explored source of endosymbyotic creativity" (Ryan, 2006: 657). Crucial according to both authors are ERVs, endogenous retroviruses which: "... have invaded the germ cell lines of every species of vertebrate. Here they replicate in Mendelian Fashion, as an integrated part of the sexual reproduction of the host, to inhabit the genome of all future generations" (Ryan, 2004: 560).

Each species of vertebrates seems to carry in its noncoding DNA regions (its so-called junk-DNA) parts and pieces if not whole sets of ERVs, that when taken together in humans, make up half of our genome (Ryan 2004: 560; Villareal, 2004: 297-298). Evolutionary geneticists are increasingly convinced that endogenous retroviruses have made a major contribution to vertebrate, primate and ultimately human evolution. In this context, Ryan (2002) has coined the term plague culling: our past is most probably characterized by repeated epidemics of exogenous retroviruses, leading to species gene pool culling and coevolution between the virus and the genotypic rudiment of host population capable of sustaining the persisting presence of the virus. In the case of retroviruses, persistence of the virus-host interaction leads to endogenization of the retrovirus, leading, in effect, to a virus-host holobiont. The endogenized virus often replicates and spreads in the host genome, extending its range and influence in the symbiogenetic union, and ultimately giving rise to major changes in translational gene expression and developmental pathways (Ryan, personal communication). Again contrary to received wisdom, these non-coding pieces of viral DNA cannot be regarded as Junk-DNA either, "... because HERVs are not acute viruses, behaving selfishly. Indeed there is growing evidence that HERVs are symbiotic

partners that have been integrated into the human genome for millions of years" (Ryan, 2004: 561).

Such changes are readily testable through molecular genetics and explain the vast numbers of viruses and virus products in the human genome. They make a major contribution to the evolution of the virus-host ensemble, with obvious implications for species formation. Ryan and Villareal therefore place themselves in a long tradition that dates back to Lederberg, who was the first to expand the term heredity to include *infective heredity* (Sapp, 2003: 243 and 2004: 1048).

Genomically, Ryan (2002: 117) therefore redefines symbiogenesis as follows: "Symbiogenesis is evolutionary change arising from the interaction of different species. It takes two major forms: endosymbiosis, in which the interaction is at the level of the genomes, and exosymbiosis, in which the interaction may be behavioural or involve the sharing of metabolites, including gene-coded products."

At the biological level, this is indeed a very useful definition and it can therefore be understood as part of a universal symbiogenetic approach. In itself, the definition cannot be understood as such a universal definition, because it excludes certain anthropological and linguistic processes that we shall return to later.

Similar to Dyson's theory on the origin of life, and contrary to the serial endo-symbiogenetic theory (Margulis, 1999) that argues that it was the merging of different prokaryotes that resulted in the origin of the nucleated cell, Villareal (2004: 304) also defends a "... viral origin of the eukaryotic nucleus". The main reason Villareal (2004: 304–305; Villareal and Defillips, 2000) gives for this view is that a comparison of all prokaryotic genes only results in 324 shared genes of which, most importantly, none are responsible for DNA replication. Viruses however are genecreating machines: 80% of the genes found in viruses are unique to these viruses and thus not derived from pro- or eukaryotic beings. Therefore Villareal hypothesizes that it was a virus that probably donated the genes responsible for replication.

The most promising application of viewing viruses as possible symbiotic partners however lies in medicine. When viruses or bacteria are being genetically engineered and induced into patients as a possible treatment, symbiogenesis is artificially applied (Ryan, personal communication).

7. Universal Symbiogenesis and Hybridization

Joshua Lederberg was the first to argue that "hereditary symbiosis in which phylogenetically distinct genomes were brought together was analogous to hybridization" (Sapp, 2003: 244). Hybridization is too often regarded as an exceptional behaviour only portrayed by plants (Gontier, 2006b). The contrary however is true. Not only different plant species but a multitude of animal species are able to

hybridize and these hybrids often can produce fertile offspring. Therefore hybridization today is more and more understood to be a mechanism that can introduce evolutionary novelty as well (Ryan, 2006).

As already argued, universal selectionist accounts take vertical evolution as the rule and horizontal evolution as the exception. In a very real sense, both views exclude each other. The biological species concept for example (Mayr, 1997) takes reproductive isolation as the criterion to divide different organisms in various species. Stated differently, it takes the possibility of hybridization, understood as horizontal mergings between different individuals, as the criterion for including individuals into a certain species. Hybridization, understood as a process that can introduce evolutionary novelty, focuses on the opposite: here the mergings are what distinguish species.

Universal symbiogenesis can also include hybridization: it results from the horizontal mergings of different entities which results in the very rapid emergence of a new variant or species. The process is also irreversible in that sense that, although the hybrid can sometimes produce one variant that lies at its origin, the hybrid itself can never undo itself from one of its *symbiotic* partners.

8. Universal Symbiogenesis and Culture

The tragedy of the nature/culture divide

Today it is an unquestioned truism that culture and nature are two completely different phenomena. The main reasons that are given by anthropologists as to why nature and culture are so different from one another, is that the former is directed by blind natural selection, where competition and survival of the fittest are the basic themes and the focus lies exclusively on the vertical transmission of traits. The latter on the contrary is characterised by wilful (rather than blind) horizontal transmissions through, amongst others, learning. Learning requires teaching and thus cooperation between the teacher and the student, if not altruism altogether since it can be very costly to share information freely. And also other communicative actions besides intentional learning can result in the horizontal transmission of cultural traits.

Unfortunately, many anthropologists (and social scientists) are not sufficiently acquainted with evolutionary theory and therefore they equate evolution with natural selection, as if that were the only mechanism through which evolution can occur. At the same time evolutionary biologists who have developed an interest in questions related to the evolution of culture, language or science, mainly focus on evolution by means of natural selection and hence contribute willingly to the dichotomization between the fields of biology and anthropology.

Yet if we were to trace the origins of the nature-cultural

divide (the name given to the disciplinary divisions that set off the natural sciences from the social sciences), a complex scenario unfolds before our eyes. A full overview of the different theories on the relation between nature and culture is beyond the scope of this article (but see Ingold, 1986: 30-73). Important for the purpose of this paper is that evolutionary biology (back then equalled with natural selection) and anthropology, as a scientific field 10, somewhat originated at the same time in western history and both developed their research programmes by opposing them to each other. In this context, this is what Kroeber, together with Franz Boas (1962) one of the founding fathers of cultural anthropology in America, had to say about culture in 1923: "Once the genetic diversification or 'evolution' has gone beyond a certain quite narrow degree, there is no more possibility of reversal and assimilation. By contrast, cultures can blend to almost any degree and not only thrive but perpetuate themselves. Classic Greek civilization was a mixture of primitive Greek, Minoan, Egyptian, and Asiatic elements. ... [T]he great part of the content of every culture is probably of foreign origin, although assimilated into a whole that works more or less coherently and is felt as a unit. However diversified or specialized a culture grows in its development, it can therefore always largely retrace its course; and it does normally do so, by absorbing more generalized content from other cultures, and thereby not only assimilating to them but to the totality or the average of human cultures" (Kroeber, 1963: 67-68).

Contrary to biological species that can be traced back to one common ancestor, cultural anthropologists argue that hum: beings, although one biological species, can portray different cultures. These cultures are not all historically related and thus are not part of one universal human culture. Rather different groups can develop particulate cultures and these then, wholly or partially, either merge or diffuse, horizontally or vertically. Rather then understanding these different cultures as monolithic and impenetrable wholes, cultures are best understood as open systems: they can merge and absorb other elements constantly. These absorption processes can, to a certain extent, be traced. The end result of these processes is often a culture with new characteristics that functions and is perceived once again as an integrated whole.

For us, the parallel with universal symbiogenesis is of course obvious: different entities fuse and the result is the emergence of an entity with new characteristics. Furthermore, cultural evolution can happen quickly: French fries and the computer concurred the world in no time. And just as the symbiotic partners in SET-theory (Margulis, 1999) can to a certain degree be traced back because of genetic sequential analyses of cyanobacteria and parracocci,

so we can trace back the origin of certain material and nonmaterial elements that make up a culture through archaeology, written history and so on.

This parallel between symbiogenesis and cultural evolution was however not that evident for the pioneering scholars working on anthropology and symbiosis. Culture was understood to be radically different from organic evolution and this eventually resulted in the idea that anthropology needed to be placed outside of biology and the hard or natural sciences altogether. For Kroeber (1965: 68), this is how culture should be portrayed (see Fig. 1): "... the course of organic evolution can be portrayed properly as a tree of life, as Darwin has called it, with trunk, limbs, branches, and twigs. The course of the development of human culture in history cannot be so described, even metaphorically. There is a constant branching-out, but the branches also grow together again, wholly or partially, all the time. Culture diverges, but it syncretizes and anastomoses too."

Today the idea that different cultures live in close contact with each other has led to an ecological approach to culture (Ingold, 1986: 40), and cultural ecology, just as biological ecology back then, was not understood as an evolutionary field.

While de Bary and Frank had already formulated their ideas on symbiosis in the late 1800s, Merezhkowsky actually lived and wrote about symbiogenesis at around the same time as Kroeber did, but their pioneering ideas on symbiosis (for an excellent overview see Sapp, Carrapiço and Zolotonosov, 2002), then as now, were just not reaching extra-biological fields and vice versa. Even today, the dichotomy of vertical/horizontal transmission of cultural traits, that goes hand in hand with debates on unilinear cultural evolution or diffusion of traits, continues to dominate current anthropological debate (see e.g. Borgerhoff Mulder, Nunn, Towner, 2006 for a recent summary).

Hybridization models of culture

Those anthropologists that did turn to evolutionary theory to model the evolution of culture(s) or cultural traits, used metaphors of hybridization to model cultural processes, a trend still distinguishable in current theorizing. For example, researchers interested in networking, multiculturalism and the (the boundaries of) ethnicity formation (Chavez, 2006; Hannerz, 1980, 1992, 2002; Pinxten and De Munter, 2006; Pinxten and Dikomitis, in press) often use metaphors based on hybridization to describe the crossings and blending of traits or beliefs. Rather than understanding culture or individual ethnicity or identity formation as one monolithic unchanging whole, these phenomena are understood to be the result of the constant interaction and interconnection of different individuals that portray a variety of ideas.

Before anthropology and sociology, as independent disciplines emerged, naturalists also investigated social and cultural phenomena from within an evolutionary context.

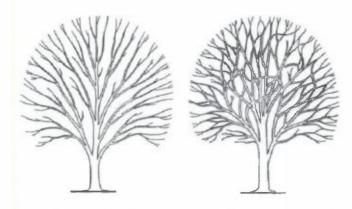


Figure 1. On the left, the organic tree of life that is characterized exclusively by diversification, on the right, the tree of culture that not only portrays branching but also merging of different evolutionary lineages. Abstracted from Kroeber (1965: 68).

Hybridization models operate alongside anthropological terms such as creolization, globalization, cyborgs, transnationality, acculturation, deculturation, culture contact, religious and ethnic shopping, which are employed to explain why it is that we read Jewish stories, use American software, dance Latin tangos, drink African coffee, watch Spanish movies, have Zen-styled apartments and so on, because this is what we call *culture*. Individuals and/or entire cultural groups, constantly pick and choose among different ways of life, ideas, cultural traits and so on; we absorb or are absorbed, are subjected or dominated by certain political ideologies, scientific theories, and so on.

Indeed, these phenomena are precisely what Kroeber had in mind when he drew his cultural tree. In fact, these processes resemble more closely the easiness with which bacteria donate and receive genetic material horizontally, how prokaryotes merge to form eukaryotic beings, and how viruses, move horizontally to penetrate hosts and create novel traits which in turn can get transmitted vertically, from generation to generation. In short, rather than applying simply the metaphor of hybridization, a universal symbiogenetic approach should be preferred. As argued above, hybridization can be classified as one aspect of a universal symbiogenetic scheme.

Hybridization models of language

Studies on language evolution are also characterised by the rise of hybridization models that complement language-as-species models (Mufwene 2002, 2005), the latter being based on neo-Darwinian population genetics. Croft (2000, 2002) was one of the first linguists to use an evolutionary epistemological model. For example, he repeatedly uses Hull's replication variation and environmental selection scheme to explain language variation. Besides this universal

selection formula, he argues for a *plantish approach* to language where language borrowing and mixing and the evolution of loan words are understood from within hybridization models.

Problems with hybridization models in language and culture

Hybridization models in culture as well as in language, however useful, are ultimately misleading. Cultures and languages are not like plant or animals species. There is for example no fixed "cultural" wild type for languages. There is no prototypical core Italian, American or Japanese culture for example: not all Italians are Catholic, not all Americans are Protestants, cowboys or Indians etc. It's difficult to define cultures because there will always be individuals who believe some ideas and use some artefacts but not others. Even the concept of family resemblances is not adequate to capture the "flow" of culture.

A universal symbiogenetic scheme however could enable us to better portray culture and language evolution (for a more extended review of the latter, see Gontier, 2006b). Just as individuals, cultures and languages are chimeras: entities stitched and patched together to form a new whole. Western secularism for example is a *symbiont* between liberalism, socialism, atheism, Christianity (itself a symbiont containing ancient Greek, Egyptian, and Jewish ideas), enlightenment-theory, and so on 11.

Just as there are no biological "... self-maintaining individuals ..." (Margulis and Sagan, 2002: 19), there are no self-maintaining cultures or languages. We are all symbionts, not just in our cells but in our way of life. Culture is indeed very much an ongoing process "... where typewriters and televisionlike screens integrate to form laptops and internal combustion engines and carriages merge to form automobiles" (Margulis and Sagan, 2002: 172). Therefore, a metaphor of universal symbiogenesis would be useful to complement the currently fast-rising universal selectionist ideas in the humanities where merging of lineages are, due to a lack of knowledge concerning different evolutionary ideas, even regarded as impossible since they don't stroke with the branching pattern set forth by Neo-Darwinian theory that focuses on natural selection.

And of course, a metaphor can only go so far. The symbiogenetic species concept for example is very precise: "We ... define a species as follows: Two living beings belong to the same species when the content and the number of integrated, formerly independent genomes that constitute them are the same" (Margulis and Sagan, 2002: 94).

¹¹ Just as the Modern Synthesis is a *symbiont* of Darwin's, Mendel's and the population geneticists' ideas.

It is indeed impossible to distinguish, let alone count, all the elements that are borrowed or mixed in a given language or culture. But this does not *a priori* entail that it is not worth the effort to examine how many elements became merged throughout the course of its history. Universal symbiogenesis would thus introduce and allow for concepts such as interaction and cooperation that often operate in the humanities, notions that are often countered by concepts of competition (see e.g. Speidel, 2000), and as such the concept of universal symbiogenesis can complement and/or counter cost-benefit equations and ideas on selfishness.

9. Conclusion

The theory of evolution by means of natural selection and universal selectionist accounts that grew out of them have turned out to be very useful tools to model the evolution of life and various products of life. However, it cannot explain all the different types in which evolution can occur and produce evolutionary novelty. If natural selection would indeed be able to explain all of life's evolution, then and only then, would it be an unscientific theory for a theory that explains everything explains nothing. The latter however is not the case.

Faultfinders have rightly argued that the Modern Synthesis focuses exclusively on the mechanism of natural selection to explain evolution. It has been argued that the Modern Synthesis presents a sterile view of evolution (Sapp, 2004: 1049) for it fails to include the microcosm, which results in an evolutionary theory only applicable to zoology (Margulis and Sagan, 2002). The focus on competition and cost-benefit equations naturally excludes cooperative and altruistic views since both are antagonistic counterparts (Speidel, 2000), and organisms as well as species are, within a (post-)neo-Darwinian view, understood to be independently evolving entities (Margulis and Sagan, 2002).

Here, symbiogenesis – which does not regard evolution as a sterile process – allows for cooperative views and, following Margulis ideas, sees all organisms as chimeras, is offered as a complementary view. Symbiogenesis can be universalized as well and can include at minimum the epidemiology of viruses, hybridization, cultural and language evolution and even certain cosmological processes. Universal symbiogenesis even has potential in medical applications. And also – not discussed here – epigenetic processes can be absorbed into a universal symbiogenetic scheme, because the different interaction of the same genes lead to the emergence of new traits and sometimes even result in speciation.

The already often used notion of a *symbiont* by scholars working within a symbiogenetic framework can thus be applied as a universal, evolutionary epistemological

concept as well, where it can complement Dawkins' replicators and Hull's interactors.

The enormous potential of an evolutionary view based on symbiogenesis is yet to be felt in many extra-biological fields and also within evolutionary biology itself. It would be an enormous waste not to explore this potential and to dismiss symbiogenesis *a priori* as a "would-be challenger" to selectionism. The universal symbiogenetic formula presented in this article will contribute in a positive way to making the importance of symbiogenesis more widely known in these other fields of research.

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