What Niche Construction is (not)

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Abstract This chapter compares standard evolutionary theory to niche construction theory, in which an organism can affect its environment and can thus influence the selective process to come. We show how to characterize this confrontation in terms of the time-scales of the processes involved, which allows us to identify the range of applicability truly proper to niche construction theory, and to suggest the existence of evolutionary phenomena that are not describable by standard evolutionary theory.

Keywords natural selection, niche construction, adaptation, extended phenotype, time-scales

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Introduction

The theory of evolution by natural selection can be traced back to Darwin and Wallace (1858) and Darwin (1859) – though of course, depending on one's taste for historical analogies, more venerable predecessors can be found (*e.g.* Empedocles, Vth c. BC (Fairbanks 1898), or more recently Sebright 1809, Matthew 1831, Thompson 1839). The theory was a charge against the immutability of species and an argument for the descent with modification, as well as an argument for taking natural selection as “the main but not exclusive means of modification” (Darwin 1859:6). Moreover, throughout Darwin's book it is clear that “above all, Darwin's mechanism of natural selection was intended to explain that which British natural theology found so significant : adaptation.” (Ruse 1992:78).
Ever since, the history of Darwin's (and Wallace's) theory has been rich (extended accounts of the story can be found in *e.g.* Mayr 1982, Sloan 2008). Two historical turns will be particularly important for us : the synthesis between genetic gradualism and natural selection as achieved by population genetics (Fisher 1930), and the synthesis between population genetics and taxonomy (Dobzhansky 1937), that would initiate the Evolutionary Synthesis in the 40's (Mayr and Provine 1980-1998:xii). The Synthesis in turn would grant the divorce between evolutionary biology and embryology, despite some good times in common of these disciplines in the past (see Amundson 2005). Most of the current debates, including the place of niche construction in evolutionary theory that we will study in details, are rooted in this story. We will come back to light historical accounts below to enlighten these roots more.
For the two or three past decades (Lewontin 1983, Olding-Smee 1988), evolutionary theory has delivered a growing movement “that has sought a re-conceptualization of adaptation by placing emphasis on niche construction” (Laland 2004:316). Niche construction is the process whereby organisms, through their metabolism, activities, choices etc, modify the selection pressures to which their or other's populations are exposed (Odling-Smee, Laland & Feldman, hereafter OLF 2003:419). Thus to the proponents of this movement, « there are in fact two logically distinct routes to the evolving match between organisms and their environments: either the organism changes to suit the environment, or the environment is changed to suit the organism.” (OLF 2003:18). “Match” here, sounds like the “adaptations” to be explained solely by natural selection in Darwin's project as summarized by Ruse's quote above. Niche construction is presented “not as just a product of evolution, but as a co-contributor, with natural selection, to the evolutionary process itself.” (OLF 2003:370). Taking niche construction into account should lead to a new, extended, evolutionary theory (OLF 2003:370-385).
In this paper, we will investigate the organism-environment symmetry introduced by niche construction, in particular as regards adaptation, and how niche construction theory introduces novelty in evolutionary biology. Most arguments will deal with verbal formalizations and sometimes, we will have to to investigate the meaning of a single word. Verbal formalizations are versatile means to account for intricate phenomena. They help us to make sense of models

(in particular mathematical models), and probably guide, or rather constrain, our empirical and theoretical explorations. Thus, in-depth treatments of verbal formalizations are a necessary evil (see notably Fox Keller 2002, *e.g.*:138). They allow to escape verbal traps, of which authors cited here are fully aware, but that could confuse naive readers. We will (briefly) see that figures or equations, that is, translations in other languages, can help but are not sufficient for our questions.

First, we will give some verbal formalism to lay the foundations for our questions (section 1). Then, we will present standard, if any standard, natural selection theory (section 2). Then, we will present and discuss niche construction theory (section 3), in particular as regards adaptation and evolutionary explanations (section 4). Finally, we will discuss its place in "alternative" evolutionary biologies (section 5), before concluding and summing up the main point (section 6).

Note: To ease reading, numerous footnotes specify details while lightening the main text. A glossary and a summary are given at the end of the text.

1. Our verbal formalism

1.1 Explanation and the many scales of biology

To start with, let us consider that an explanation consists of an invariant link between different (at least two) states of a system, *e.g.* some initial conditions and some outcome (Woodward 1997, 2001). Investigating the diverse possible forms of the invariant link falls out the reach of this paper, let us just notice that for the explanation to be relevant, the invariant must usually link as few outcomes as possible to given input variables[1], for some cost in parsimony. In this paper, we will consider that the invariant is the *explanans*, *i.e.* the part of the explanation that *explains*, and that the states are the *explanandum*, *i.e.* the part that *is* explained[2]. Building the explanation consists in particular to define which part of the system belongs either to the invariant or to the state, for both the *explanans* and the *explanandum* will change if some part of the invariant becomes a variable or vice versa. Thus, there is a fundamental asymmetry between the invariant and the set of states, deeply rooted in what an explanation is. This question will turn out to be crucial in the next parts.

Except in the case of a theory of everything, explanations are local[3] : they have a limited

1 For instance, the case where every possible outcome are linked to every possible input variables is a tautology. In our opinion tautologies are not considered as explanatory, even in everyday life.

2 One could argue that the *explanans* contains also the initial conditions, and that the *explanandum* contains only the output state. There can be reasons not to do so (in particular when it is desirable to keep an explanatory symmetry between initial and final states, *e.g.* when the invariant is a bijection). More generally, the rationale for equating invariance and *explanans*, is to consider that the invariant structures (makes sense of) the set of states. Anyway, this consideration does not affect the argument here.

3 Here we mean local in a similar sense than Van Frasen means abstraction below. In particular in Van Frasen's example about Caesar's death, the abstraction is valid relatively to a given time-scale.

"The description of some account as an explanation of a given fact or event, is incomplete. It can only be an explanation with respect to a certain relevance relation and a certain contrast-class. These are contextual factors, in that they are determined neither by the totality of accepted scientific theories, nor by the event range of validity (that is a limited range of definition and, if locally defined, of sufficient accuracy). The range can be defined in terms of scales on given dimensions (spatial, temporal, etc), and/or of objects of study (microtubules, micro-organisms, etc), or else. Assessing the range of validity of an explanation is a matter of betting (*sensu* Godfrey-Smith 1998:53), because knowing the range would require to know that everything is known, though it is crucial to rumble where the explanation holds and where it does not.

The biological explanations we will be concerned with in this paper deal with dynamical systems and are time-scale dependent. The invariant in a dynamical system is the law of transformation that enables one to predict, given some state, a later state (or retrodict a previous state). The invariant includes parameters and everything else in the explanation that does not depend on time. On the other hand, the state of the system is the set of the time-dependent variables, at a given time.

However, the invariant generally varies beyond, or below, some time-scale. The usual way to simplify the problem is to deliberately limit the range of the explanation by assessing a time-scale separation between, say, fast and slow processes, and to consider that processes beyond or below the scale of study are invariant (for instance the laws of physics are invariant on the human time scale even if at the scale of the universe, they may have changed). Thus, different disciplines working each on a different scale will usually produce different explanations, which can in turn help them segregate into separate fields. This is the drama played by the explanations considered in this paper.

Here, we will consider several biological processes : mutation (very briefly), ontogeny, ecology, and (micro and macro) evolution. These processes are each usually associated with a corresponding time-scale, and, as we shall see, these time-scales are usually assumed to be separated. It is worth noticing that time, here, does not mean the physical time, but rather some biological time : generally the metrics involves the generation[1]. As different living systems typically have different generation-length, a given intra-generation explanation about some system (*e.g.* some vertebrate) may well deal with physical durations that represent inter-generational term for other systems (*e.g.* some gut microbes). Thus, the expressions “small time-scale” or “long time-scale” have here to be understood relatively to a given system.

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or fact for which an explanation is requested. It is sometimes said that an Omniscient Being would have a complete explanation, whereas these contextual factors only bespeak our limitations due to which we can only grasp one part or aspect of the complete explanation at any given time. But this is a mistake. If the Omniscient Being has no specific interests (legal, medical, economic; or just an interest in optics or thermodynamics rather than chemistry) and does not abstract (so that he never thinks of Caesar's death qua multiple stabbing, or qua assassination), then no why-questions ever arise for him in any way at all—and he does not have any explanation in the sense that we have explanations. If he does have interests, and does abstract from individual peculiarities in his thinking about the world, then his why-questions are as essentially context-dependent as ours. In either case, his advantage is that he always has all the information needed to answer any specific explanation request. But that information is, in and by itself, not an explanation; just as a person cannot be said to be older, or a neighbour, except in relation to others.” (Van Fraasen 1980:130).

1 For a thought-provoking, deeply worked out, work on biological time, see Bailly *et al.* (forthcoming). Bailly *et al.* propose to account for all intrinsically cyclic biological processes by adding to the physical time t, a 2nd time dimension (Θ? the “biological time”), which would be, roughly speaking, kind of a circle.

1.2 The war raging between the inside and the outside

Most biological systems are spatially delineated (even by blurred boundaries), thus defining an (external) environment of the system. Facing this inside/outside dichotomy, it may be tempting to give one side more explanatory power than the other (Godfrey-Smith 1998:51). We can distinguish several types of explanations according to the spatial localisation of the input variables[1] (*ibid.* p.30) : (1) an explanation of some properties internal to the system framed in terms of other internal properties is called *internalist* (*e.g.* gene determinism) (2) an explanation of internal properties in terms of external (*i.e.* environmental) properties is called *externalist* (*e.g.* adaptationism) (3) an explanation of external properties in terms of internal properties is called *constructive* (*e.g.* ecosystem engineering, Jones *et al.* 1994), this is the converse of an externalist explanation (4) an explanation of internal or external properties, or both, in terms of both internal *and* external properties is called *interactionist* (*e.g.* reaction norms). Externalism and internalism can thus be seen as limiting cases of interactionism[2].

Of course, living systems do not exist *ex nihilo*, outside of any environment, nor do they have no intrinsic properties constraining (defining) their response to the environment. Providing an internalist (resp. externalist) explanation is a bet : it consists in betting (*sensu* Godfrey-Smith 1998:53) that the considered internal (resp. external) variables will suffice to predict the focal output variables. The interactionist view, by contrast, emphasizes that for some imaginable values of external (resp. internal) variables, the considered input variables should be insufficient (of course, the argument also holds for imaginable values of other internal – resp. external – ignored variables), and, thus, that the given internalist (resp. externalist) explanation should have a range of validity "too much" limited by the *ceteris paribus* conditions on the ignored variables[3]. The interactionist view is particularly suited for non-linear interactions between the inside and the outside, for then small perturbations of the *ceteris paribus* conditions on ignored variables can have large effects. Like any other explanatory choice, choosing an internalist, externalist or interactionist explanation of a given living system is a matter of desired parsimony and betting about the range of sufficient

1 We assume that, in a given explanation, *invariants* are not spatially localized (as they are not temporally localized). It would seem unnecessary, for instance, to assume that in a Newtonian space the gravity law belongs to the objects with non-zero mass, or that a given metabolic law is contained in some set of cells. Of course invariants of different explanations dealing with different objects at different locations can be different. When comparing different systems, it may be tempting to compare their respective invariants. It is crucial then to be clear about the fact that these former invariants are new variables in the comparative process.

2 Interactionists : see Piaget 1971, Waddington 1975, Oyama 1985 (cited by Godfrey-Smith 1998:54).

3 A paradigmatic example of such a betting activity is given by heritability studies of the phenylketonuria (PKU). If the studied population contains homozygotes for the recessive, lethal, allele and is subject to a phenylalanine-rich diet, the genotype will explain all the phenotype, hence an internalist explanation will hold. By contrast, if the studied population only contains homozygotes for the recessive allele and some of them only are subject to phenylalanine-rich diets, then the environmental conditions will explain any difference in phenotype (externalist explanation). An interactionist explanation would explore the reaction norm and would suffer from less *ceteris paribus* conditions, but note that it would be less parsimonious too, as it would include both environmental and internal variables. These two limiting cases illustrate why heritability estimates are limited by the *ceteris paribus* conditions on the distribution of genotypes among given environments, while reaction norms are not (see Lewontin 1974).

accuracy (and definition), of the supposed type of interactions and, last but not least, of the kind of internal or external variability that is available in the given living system to explain[1].

Turning back to the dynamical biological systems, why is the internalist/externalist distinction important ? Because, to state it generally, living systems are dynamical systems that engage into *diachronic* interactions with their environment.

When dealing with such an interaction, one obvious intuition is to consider that the environment is large compared to the system, and thus (please notice that this is an intuitive and somewhat weak "thus"), that the environmental rate of change is slow compared with the system's rate of change. In particular, if the system is expected to exert some force on its environment, the effects on the environment are supposed to be small and negligible. Thereby, this intuition leads to consider that there is a time-scale separation between the fast internal processes, and the slow environmental processes[2]. For instance, when studying plant growth, we consider Earth's effects on amyloplasts distribution in statocytes, which leads to gravitropism (Wise & Hoober 2007:515), but we do not consider the effects of individual plant growth on the distribution of mass at the surface of the Earth. This amounts to considering that environmental variables may be input variables (or not, if the environment is held constant[3]), but *not* output variables, in other terms, this intuition leads to provide non-constructive explanations. In the next sections, we will examine the avatars and consequences of such an intuition. Now, keeping this formalism in mind, we are going to discuss the selectionist scheme in evolutionary biology.

2. The selectionist scheme(s) in biology

This sections does not aim at providing a full account of the structure of evolutionary theory, nor at reviewing extensively the family of models built in it. Rather, the goal here is to highlight several salient features of the selectionist scheme[4].

2.1 The scheme

The selectionist scheme can be sketched as the fulfilment of the following two conditions[5]: (1)

1 The trick here is that the available variability is investigated regarding the bet on it. If a researcher supposes that a genetic explanation will be the most appropriate for some trait (for instance, developmental clocks), he will be inclined to try to produce genetic variants for this trait, thus reinforcing the available internal variability.

2 This intuition may be reinforced in biology by the feeling that abiota is somehow inert, by contrast with living systems.

3 We mean here "constant" over the whole range of the considered objects to explain. In particular, when dealing with several biological samples, if the environment is variable from one sample to another (even if it is held constant for each sample), the environment can well be an input variable when aiming at comparing the samples (*e.g.* in studies on evolutionary convergence).

4 We purposely avoid the term "Darwinian scheme" here, fully agreeing with Lewontin (1974) : "… the essential nature of the Darwinian revolution was neither the introduction of evolutionism as a world view (since historically that is not the case) nor the emphasis on natural selection as the main motive force in evolution (since empirically that may not be the case), but rather the replacement of a metaphysical view of variation among organisms by a materialistic view.". Fisher (1930, vii) made the same point.

5 This sketch is drawn from Lewontin (1970), though Lewontin's account is slightly different : "1. Different individuals in a population have different morphologies, physiologies, and behaviors (phenotypic

the existence of some *heritable* phenotypic variability among the individuals (whatever "individual" means) in the population (2) a determined relation (at a given point in time) between the considered phenotypic differences and some differences in *fitness*.

A population fulfilling these conditions is expected to undergo natural selection. The two keywords here, which will be at the centre of the argument, are heritability and fitness (or selection). Sketching their stories quickly will help to understand which historical assumptions some current theorists would like to relax.

2.2 Historical perspectives

The substrate of heritability

Heritability has been historically central to Darwinism. The principle of "unity of descent", independently from any natural selection principle, has been used by Darwin to explain the "unity of type", that is, the resemblance of structure between organisms (Darwin 1859:206), which had been a critical issue for palaeontology and comparative anatomy during the XIXth century (Sloan 2008).

Heritability has here to be understood *sensu* Galton (1869), as any correlation[1] across generations (heritability thus entails variability : there is no correlation if there is no variation), and not in terms of any specified mechanism of inheritance. However, part of the story of biology during the XXth century has precisely been to look for the mechanisms of inheritance in living systems (see Maienschein 1992), as well as to specify in which cases the inherited materials could lead to inherited differences in traits (see Wade 1992).

For Darwin, inheritance could be a blending process involving entities (named gemmules) «

variation). 2. Different phenotypes have different rates of survival and reproduction in different environments (differential fitness). 3. There is a correlation between parents and offspring in the contribution of each to future generations (fitness is heritable)."

Lewontin puts the emphasis on heritability of fitness differences, while we put the emphasis on heritability of phenotypic differences, provided that fitness is defined at each generation. Lewontin's goal in focusing on fitness here is to dismiss neutral phenotypes as irrelevant for the scheme. Lewontin does not specify the kind of the relationship between phenotype and fitness here (loose correlation, strict bijection, etc), neither do we. For the sake of exactness, if these relations are correlations, it is worth emphasizing that correlations are not transitive (that is, "A correlated to B & B correlated to C" does not imply "A correlated to C"). Thus heritable phenotypic differences which would be themselves correlated to differences in fitness would not entail heritable differences in fitness.

1 It has often be stressed (e.g. Hull 1988 :404) that "correlation is not strong enough for heritability. The correlations must be causal.". Without entering into details here, we do not see anything else in "causation" than robust correlations (for instance : robust against different background conditions or different conditionals). However, unless when heritability is defined as the response to selection (breeder's equation : $H^2 = R/S$), the condition on inheritance is actually necessary but not sufficient, for the effects of selection to be conserved across generations (because of the non-transitivity of correlations, see section 3.2). Unfortunately, when inheritance is defined as the response to selection, the condition turns into a tautology ("effects of selection are conserved if there is response to selection") – unless, of course, we are provided with past measures of the response to selection that we can extrapolate. For reviews of classical concepts of heritability, see Wade (1992), Feldman (1992), and Visscher *et al.* (2008), for a discussion of inclusive heritability (combining genetic and non-genetic inheritance) see Danchin and Wagner (2010).

collected from all parts of the system to constitute the sexual elements” (1868:374). However, since the work of Hugo de Vries and Carl Correns in the early 1900 rediscovering Mendel's laws of inheritance (1866), the substrate of inheritance has been supposed to be non-blending entities, separate units of heredity that were named genes (after Johannsen 1909). (Here, we gloss over essential, but innumerable, historical complexities, such that the arguments of Pearson's school (1904) on the means to obtain discontinuous inheritance from blending entities.) Implicitly, Mendel's laws required a separation between the processes of inheritance on the one hand, and the ontogenetic processes on the other hand (Lewontin 1992), a separation that has been achieved in the semantic domain by Johannsen (1911), coining the terms *genotype* and *phenotype* for the first and second processes respectively. Morgan (1917) then hypothesized that genes resided at particular locations on chromosomes, and Avery *et al.* (1944) showed that (some) genes were made up of DNA, specifying a little bit more the physical substrate of inheritance. Crick (1957) postulated some years later that information, equated here as a precise sequence of bases or amino acids[1], could only be transferred *from* nucleic acid (to other nucleic acids or to proteins), but not from proteins (to other proteins or to nucleic acids)[2]. And as genes were supposed to be the only substrate for inheritance and were thought to be effectively made up of amino acids, Crick's postulate offered a support to Weismann's principle (1889:392-409) that acquired phenotypic characteristics could not be inherited (a principle, as mentioned earlier, already latent in Mendel's laws). Historically, this principle has been important to dismiss the still ongoing Lamarckism (see Bowler 1992, Sloan 2008).

The road-story of the gene concept did not end up here, and had many avatars, particularly in molecular biology (reviewed in Gerstein *et al.* 2007). Interestingly, current molecular biologists seem to no longer explicitly mention inheritance in their gene concept(s), rather defined in terms of a functional unit, which can be distributed throughout the genome[3] [4] (see also Fox Keller 2000).

Thereby, part of the history of biology during the last century has been to investigate a (time-scale) separation between the dynamics, here meant as the individual dynamics of *one* entity, of long lasting hereditary entities (the genes), assumed to remain unchanged throughout generations except by supposedly rare accidents (mutations), and short lasting, mortal, entities (the phenotypes), whose individual dynamics, also named ontogenesis, were supposed to let the long lasting hereditary entities virtually unchanged.

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1 “Information means here the *precise* determination of sequence, either of bases in the nucleic acid or of amino acid residues in the protein.” (Crick 1957, quoted in Judson 1979)

2 If information is to mean anything (for the sake of the argument, let's suppose it does), the fact that nucleic acids bear information requires itself an explanation. The classical view (see *e.g.* Laland 2004) is that *populations* of genes get informed through natural selection at the *intergenerational scale*. Thus the transfer of information *to* genes is possible in the selectionist framework, but at another level than the individual sequence.

3 See for instance the definition proposed by Gerstein *et al.* (2007) : “A gene is a union of genomic sequences encoding a coherent set of potentially overlapping functional products.”

4 By contrast, Kitcher (1992) has argued that we do not need to specify *a priori* segmentation rules for nucleic acids, dropping talk of genes and studying instead the properties of regions of nucleic acid - as long as, for evolutionary studies, the segments retained obey the rules of population genetics. This position resonates with Dawkins' (1976) and Williams' (1966).

The object of selection

In parallel with the development of genetics, Fisher (1930) provided the first synthesis of Darwinian selection and Mendelian genetics, giving birth to what is now known as population genetics. Fisher (*e.g.* 1918) was mainly interested in additive genetic effects on phenotype, which were heritable[1] and could respond to selection, by contrast with dominance and epistatic genetic effects[2], which were compared to environmental noise by Fisher (Fisher 1930:xiii, Wade 1992, Okasha 2008). Wright (*e.g.* 1921, 1930, 1932) developed similar approaches, but put an emphasis on epistasis and ruggedness of adaptive landscapes. Moreover, focusing on additivity of genetic effects somehow sustained gradualism (*e.g.* Fisher 1930:37[3]), the view according to which major evolutionary changes, described by palaeontology, can be explained by accumulation of small evolutionary changes, described by population genetics. Gradualism had already been embraced by Darwin (1859, but see 1866:132 for a "saltationist" hypothesis[4]) and had been a major subject of contention between Biometrical and Mendelian schools at the beginning of the century (Sloan 2008). Gradualism would turn out to be one of the main points of the so-called Modern Synthesis of the 30's-40's between Mendelian and population genetics, cytology, ecology, systematics and paleontology (Mayr & Provine 1998).

Notably, embryology had not been included in the Modern Synthesis, despite some embryological works of the founding fathers (Huxley 1932, Huxley and de Beer 1934, Wright 1934), and despite the fact that the founding fathers were well aware of its importance (*e.g.* Huxley 1942:8, Mayr 1970:108). Reciprocally, embryologists of the early XXth century did not care much about evolution, rather focusing on mechanisms of development (for a review on the (non-)relation between the Synthesis and embryology, see Hamburger 1998). The separation between development and evolution culminated particularly in Mayr's dichotomy between two biologies (1961, 1982:67) : the biology studying *proximate* (developmental) causes and the biology studying *ultimate* (evolutionary) causes : "Proximate causes have to do with the decoding of the program of a given individual ; evolutionary causes have to do with the changes of genetic programs through time, and with the reasons for these changes" (Mayr 1982:68). To Mayr, the two biologies were both "remarkably self contained" (1982:68) and necessarily complementary (1982:72,131), but the two kinds of causation were *not* to be confused (1982:11,455,834). Noteworthily, this dichotomy was implicitly posed in terms of time-scale separation.

At that time, for most population geneticists and supporters of the Modern Synthesis,

1 See "narrow sense heritability" in Lewontin (1974)

2 See "broad sense heritability" in Lewontin (1974)

3 The famous quote is : "Evolutionary changes are generally recognized as producing progressively higher organization in the organic world." (Fisher 1930:37)

4 "But I must here remark that I do not suppose that the process ever goes on so regularly as is represented in the diagram, though in itself made somewhat irregular, nor that it goes on continuously; it is far more probable that each form remains for long periods unaltered, and then again undergoes modification. Nor do I suppose that the most divergent varieties are invariably preserved: a medium form may often long endure, and may or may not produce more than one modified descendant; for natural selection will always act according to the nature of the places which are either unoccupied or not perfectly occupied by other beings; and this will depend on infinitely complex relations." (Darwin 1866:132). This sentence appears in this (*i.e.* fourth) edition of *The Origin*.

theorizing evolution would imply to focus on genes frequencies (*e.g.* Dobzhansky 1937:11, defined evolution as a change in gene ratios, a view still dominating (Rosenberg and Bouchard 2002-2008)). The gene-centred perspective gained much interest a few decades later, with the "unit of selection" debate between gene-selectionists (e.g. Williams 1966, Dawkins 1976), claiming that genes were the genuine units of selection, and organism (or group or species) selectionists, claiming that organisms, groups or species were the relevant units to consider for selection studies (*e.g.* Lewontin 1970, 1974, Gould 1977, for species selection see Vrba 1984, Jablonski 1986).

The debate could be quickly sketched as follow[1] (here we give only a rough account of the debate to put our section 3.5 in perspective ; we have to ignore primary but dense historical subtelties, interested readers can refer to *e.g.* Okasha 2006, Huneman 2010:348-351). Gene-selectionists claimed that no matter how much and how complicated interactions between loci, it would always be possible to identify a *mean effect* of any given gene substitution at a given locus, on fitness at the population level (Williams 1966:57). Moreover, selection at a higher level than the gene (*e.g.* selection for altruistic traits in a group) would suffer from dynamical impediments, because evolutionary dynamics at lower levels (*e.g.* genes) were thought to be in general so much faster than dynamics at higher levels (*e.g.* groups), that they would prevent most of the selection processes to be relevant at higher levels (Williams 1966,

1 The two positions are illustrated by this two following quotes :

The first : "Obviously it is unrealistic to believe that a gene actually exists in its own world with no complications other than abstract selection coefficients and mutation rates. The unity of the genotype and the functional subordination of the individual genes to each other and to their surroundings would seem, at first sight, to invalidate the one-locus model of natural selection. Actually these considerations do not bear on the basic postulates of the theory. No matter how functionally dependent a gene may be, and no matter how complicated its interactions with other genes and environmental factors, it must always be true that a given gene substitution will have an arithmetic mean effect on fitness in any population. One allele can always be regarded as having a certain selection coefficient relative to another at the same locus at any given point in time. Such coefficients are numbers that can be treated algebraically, and conclusions inferred for one locus can bi iterated over all loci. Adaptation can thus be attributed to the effect of selection acting independently at each locus. Although this theory is conceptually simple and logically complete, it is seldom simple in practice and seldom provides complete answers to biological problems. Not only do gene interactions and the processes of producing phenotypic effects offer a universe of problems for physiological geneticists, but the environment itself is a complex and varying system. Selection coefficients can be expected to change continually in all but the most stable environments, and to do so independently at each locus." (Williams 1966:56-57).

The second : "It must be remembered that each locus is not subject to selection separate from the others, so that thousands of selective processes would be summed as if they were individual events. The entire individual organism, not the chromosomal locus, it the unit of selection, and the alleles at different loci interact in complex ways to yield the final product." (Ayala 1978:64 quoted by Hull 1988:217).

Here, Williams argues that at the population level a selective effect, no matter how small, will take place on each locus, while Ayala remarks that if selection is a screening process, the holes must have the size of organisms, not genes. But this does *not* contradict Williams arguing about processes at the population level.

The contradiction would rather come from non-repeatability of selection events if the interactions between loci, and environmental changes, were too strong and the population too small : selection coefficient would be inconsistent throughout generations and the dynamics, even if highly selective, would look like drift (here with a high variance in offspring between individuals). Or, at the level of empirical sufficiency, the contradiction could come from the possible non-usability of the theory (see Lewontin 1974:9).

Lewontin 1970, but for selection at the species level see Jablonski 1986). The claim of gene-selectionists was that *reducing* evolution to gene dynamics should be successful (Hull 1988:422, Godfrey-Smith 2000:4). By contrast, organism-selectionists highlighted that "selection does not see genes" but for instance whole organisms, and that interactions between elements at all levels (mostly between loci in a genome, but also between organisms, groups, etc) were evolutionarily significant (the debate still goes on : the above, now quite colloquial, quote on selection has been found in Minelli 2009:207). Most notably, Darwin himself had not been sharp on this issue, endlessly speaking of the evolution of *variations* (*e.g.* 1859:12, 84), but in the meantime speaking of nature selecting variations for "the good of" the individual (*e.g.* 1859:84), the group (*e.g.* 1859:202) or the species (*e.g.* 1859:201)[1].

As Hull (1980:313, 1988:217) has pointed out, most of the (bloody) debate arose because of an ambiguity in the phrase "unit of selection" : gene selectionists actually meant that genes were units of *replication*, fully aware (at least officially : Hull 1988:422) that selection coefficients should come from phenotypic effects (*e.g.* Williams 1966:57)[2], while organism selectionists meant that organisms were units of *interaction* with the world (*sensu* Hull 1980:318), most of them fully agreeing that genes were the units of replication (Mameli 2004:37, see e.g. Lewontin 1970:14[3]). *A posteriori*, the debate could seem pointless, but words matter : for gene selectionists proposed to frame evolutionary theories without any reference to interactions, focusing in particular on the bookkeeping of gene frequencies (Williams 1985), while organism selectionists urged not to evacuate from evolutionary biology development and/or causal mechanisms leading to selection (Mayr 1978, Gould and Lewontin 1979, Hull 1988:218, 422). As for developmental mechanisms, in the meantime evolutionary developmental biology (evo-devo) (re)-emerged as a distinct field of research in the 80's – partly as a resurgence of the earlier developmental genetics of Morgan (1926:510) and Goldschmidt 1940 (for a thought-provoking review on the historical relationships between embryology and evolutionary biology, see Amundson 2005). We will return to the issue of evo-devo later.

In conclusion, XXth century evolutionary biology has been stretched between an inclination to consider development as a black box and separate it, at least temporarily (that is, for some decades), from evolution, as did the Modern Synthesis and in particular gene-selectionists[4], and an inclination to do the converse.

1 We let to reader's discretion the interpretation of Darwin's writings in terms of replicators (the variations) and interactors (individuals and groups).

2 Indeed, population genetics alone is insufficient to determine the values of particular selection coefficients, or to provide explanations that developmental studies could provide (*e.g.* the fact that developmental constraints could lead to evolutionary stasis, see *e.g.* Gould and Lewontin 1979).

3 Even when dealing with the theoretical possibility of selection at the level of the population, Lewontin frames the debate in genetic terms : "In this case the genetic composition of the species is a result of the more or less equal interaction of powerful selection at three levels." (1970:14). The three levels here are : organelle, individual, and deme.

4 Being a supporter of the Synthesis does not imply to be gene-selectionist. For instance, Mayr was far to be a gene-selectionist : « By the 1980s the geneticists had given up their endorsement of the gene as the object of selection, and the synthesis can be considered fully completed only now." (Mayr & Provine 1998:xiii).

2.3 The selectionist scheme revisited

Historical accounts above have left us with several dichotomies that we will find useful to cast the problem, and specify the selectionist scheme in the dominant view. (These dichotomies, among others, have been critically reviewed in Amundson 2005 and Laland *et al.* 2008, but these critics should not affect the presentation here. Besides, we will discuss these dichotomies ourselves throughout the presentation.)

Heredity and replication

For the scheme to be applied across generations, (variable) long-lasting, *i.e.* hereditary across generations, entities must be exhibited. With analogy to Weismann's separation between the (potentially immortal) germen and the (always mortal) soma of metazoans, such entities has been qualified *germline* (Dawkins 1976-2006:172,258).
Following Darwin (1859:Chap.III) evolutionary biologists focused on entities (mainly organisms and, later, genes) having geometrical rates of increase (in absence of any limiting factor), that is, entities having somehow autocatalytic qualities. Indeed, geometrical dynamics favour competition and replacement of some variants by others, thus enhancing the relevance of considering such autocatalytic entities to explain a given state of the living world[1]. Such autocatalytic entities, faithfully reproducing (some of) their own variations, have been named *replicators* (Dawkins 1976-2006:Chap.2, 1978).
Genes have been considered as the most paradigmatic units of heredity (as Mendelian characters) or of replication (as strands of nucleic acids). Because of mutation and recombination that can break up a given sequence, the smallest unit of replication can be a single nucleic base, but larger strands can also be considered provided that they are sufficiently variable, and sufficiently stably transmitted and/or sufficiently affected by selection to overcome the degradation dynamics caused by mutation and recombination (Williams 1966:24, Dawkins 1976-2006:36, Kitcher 1992). By contrast, organisms (or groups) are considered too ephemeral and unable to pass on changes in their individual structure, to play a role as replicators. Asexual organisms (*sensu* organisms reproducing asexually) seem to be a notable exception to this account, but they should not, if their non-genetic materials have faster enough (degradation) dynamics compared to the evolutionary dynamics described in terms of long-lasting entities.
It is worth noticing that, even if the replicator concept has been designed to generalize the properties of genes, anything else eligible to be a replicator can be included into evolutionary studies, including cultural entities (Dawkins 1979, 2004) : the selectionist scheme (but not particular models) is at first sight left unchanged whatever the selected object is.

1 “Replacement” occurs even in a world with no limiting factors. This is because two lineages should never have exactly the same geometrical rate of increase (axiom of inequality, Hardin 1960), and because the difference between two exponential growths is itself an exponential. Thus, one lineage will exclude the other in the space of frequencies (which is actually a limiting space).
By geometrical dynamics, we mean also differential mortality (even without any reproduction), or growth of organisms or of parts of organisms.

Phenotypes of replicators (development)

For the replicators to be relevant, they must exert an influence on the world : that is, they must have *phenotypes* (they must be *active* germline replicators, Dawkins 1982:47). Besides, these phenotypes must be relevant to us and (sufficiently) knowable. A phenotype is the response of a gene to the environment. Generally speaking, a phenotype must be understood as a part of the reaction norm plotted on environmental dimensions (Lewontin 1974-2006):

$$p = \mathrm{o}(g, E)$$

where *p* is the phenotype of a gene *g* in an environment *E* given by an ontogenesis function *o*. (Noteworthily, the reaction norm can be refined by explicitly showing developmental noise rather than averaging it.) The environment here should include other replicators, competitors or not (*e.g.* other genes of the same genome, Dawkins 1976-2006:ix) and could be highly multidimensional because of non-additive effects, which forbid easy *ceteris paribus* averaging on environmental dimensions. Thus, if the "environment" varies through time (on a intra or intergenerational time scale, see section 3.10), the net effect of the replicator on the world will typically depend on the selected time window.

However, because investigating reaction norms implies to empirically set and replicate all considered variable environmental conditions (including the rest of the genetic background), and because theoretical investigation of complex development can quickly become intractable, there is a temptation to rather consider the environment (at least the rest of the genome) as constant, irrelevant, or averaged over (*i.e.* treated as random noise with no mean effect). This averaging actually relies on the assumption that organisms, and living systems in general, can be "atomized into partial phenotypes and partial genotypes" (Lewontin 1992:140), while, in parallel, the environment can be atomized into "an array of factors" (Bock 1980).

We already mentioned above Williams' thinking of selection in terms of differences in average effect on fitness (1966:57). A close thinking is exemplified with regard to development by, for example, this quote of Dawkins : "Expressions like 'gene for long legs' [should be understood as] a single gene which, *other things being equal*, tends to make legs longer than they would have been under the influence of the gene's allele" (1976-2006:37, Dawkins' emphasis). Elsewhere, Dawkins (2004:392) explicitly calls for using analysis of variance to sort out differential effects from complex developmental interactions.

Unfortunately exhibiting such a genotype-phenotype mapping is impossible except in very special cases (Lewontin 1992). Analysis of variance is a method of description which is not robust enough against usual *ceteris paribus* relaxations on environmental and genetic backgrounds to serve as a predictive method of effects of gene substitutions in an evolutionary process (Lewontin 1974, 1974-2006). For the sake of argument, let's suppose for the moment that the genotype-phenotype pathway is well defined and accessible to knowledge (but see section 3.11 and 5.5).

It should be noticed that here, "phenotype" means any effect on the environment *of a gene* (or more generally a replicator) that is attributable to the given gene, and not effects that would be contained below organism's boundaries[1]. Phenotypes can be indefinitely extended spatially

1 For clarity, we however exclude replicating events as phenotypic effets. They would seem eligible (they indeed are events on the world), but the conceptual distinction between the genotype and the phenotype

provided that the considered environmental modification can be attributed to the presence of a given gene (Dawkins 1978, 1982), whatever the importance of boundaries in particular evolutionary processes. (Here, we do not follow Sterelny's argument (2005), who restricts extended phenotypes to such environmental features that are systematically and pervasively controlled, and that are "central to the organism's life history". We prefer not to presume what kind of environmental modifications will be evolutionarily relevant, in particular because relevance here depends on the time-scales of interest.) Besides, because they are effects on the world of an entity, phenotypes are always spatially extended with regard to this entity (even if this spatial extension is at the molecular scale, as with transposons). Spatial extension will be further discussed (section 2.4, 3.9, 3.13).

Variations in fitness (evolution)

For phenotypes to undergo a selective process, they must have different *fitnesses*[1]. Several accounts of what fitness should mean have emerged (discussed *e.g.* in Endler 1986:33-50, Beatty 1992, Paul 1992, Fox Keller 1992, Ariew & Lewontin 2004, Bouchard 2008, Rosenberg & Bouchard 2002-2008, Huneman *in prep*.). Examining them in detail falls out of the scope of this study, because the question here will be less about what fitness means than about what determines fitness, and what fitness determines. However, to avoid confusing the reader by using undefined keywords, we will nevertheless specify the interpretation we choose. Besides, this issue is closely related to the issue of adaptation (section 4.1). The key here, is that fitness should have an explanatory value of dynamical trends in the selectionist scheme, by contrast with mere by-products of incidental dynamics[2] (see Bouchard 2008).

Preliminary note : We will not specify whether fitness is given at the individual level (fitness of an individual with regard to the considered phenotype) or at some population level (mean fitness of a given phenotype). Indeed, this question is orthogonal to ours here : we will deal with trends, not with noise – whatever, besides, the importance of noise in evolutionary processes. To state it quickly, given a selective trend, we can go from an infinite population of identical individuals (identical here with regard to a given measured phenotype) to a population reduced to a single individual by decreasing the number of sampled individuals, without modifying the selective trend (let aside, of course, density-dependent selective trends).

To get an intuitive idea of what an explanatory concept of fitness should be, we can cast the

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make it hard (though not impossible) to see offspring replicators as phenotypes of the parent replicator.

1 Actually, a comparable account would hold if there were no variation. Of course, there is no "selection" if a (population of a) single variant is involved, but we may still be interested in some comparable trends (absolute growth or subsistence for instance). Darwin himself considered the two cases, competition between variants and (lonely) subsistence (1859:62) :

"Two canine animals in a time of dearth, may be truly said to struggle with each other which shall get food and live. But a plant on the edge of a desert is said to struggle for life against the drought, though more properly it should be said to be dependent on the moisture."

2 The concept exposed here belongs to the family of so-called "ecological fitness" concepts, dealing with interaction properties of the phenotype ; by contrast with definitions of fitness in terms of observed *past* success.

fitness concept into solving/problems terms. On this view, Bouchard[1] (2008:561) gives : "*a* is fitter than *b* in *E* = a's traits result in its solving the design problems set by *E* more fully than *b*'s traits"[2]. To remain consistent with our previous terminology, we just have to cast the definition in terms of phenotypes[3]. And as we deal with dynamical trajectories, we have to specify the time-interval on which the definition is applied. Thus we obtain : "a phenotype *a* is fitter than a phenotype *b* in *E* if it solves the design problems set by *E* on a time interval *T* more fully than *b*". The design-problems set by *E* possibly include an interaction between *a* and *b*. To include the time-interval is vital here, because the selective trends will generally depend on it (Sober 2001:4)[4]. Typically, population genetics defines fitness relatively to one single, complete, generation – though, most empirical studies actually deal with intragenerational intervals (on this issue see Endler 1986:12,40,49,84,206). For the moment, we will follow population geneticists and consider the time-interval *T* to be of one generation.
Noteworthily, for the scheme to be physical and not metaphysical, the fitness must be approximately measurable ; for the moment, we will assume it is. Assessing fitnesses of phenotypes results in a phenotype-fitness map[5]. It is usually assumed that fitness depends on the environment : indeed one of the primary aims of the selectionist scheme is precisely to explain why organisms fit their environment (*e.g.* Endler 1986:32). Thus generally speaking, the dimensions of the phenotype-fitness map will include environmental conditions, and the fitness of a given phenotype will be comparable to a reaction norm against every environmental conditions to be considered:

$$w = s(p, E)$$

where w stands for the fitness of a phenotype p in an environment E, as a result of the selective function s. The "environment" here, can include other phenotypes and in particular the competing variants. (That the number of different environmental conditions to consider could go to infinity is a problem to implement the scheme on real cases, but let's assume for the moment that the biologist will be able to extract a limited set of relevant environmental conditions.)
As we mentioned earlier, a striking aspect of the selectionist scheme is that it typically involves geometrical dynamics, proper to lead to rapid exclusion/replacement of variants (and accumulation of changes in a gradualist view). The effect of fitness we will be interested in, is

1 This is a slight modification of Dennett's definition (1996). It corresponds to adaptedness *sensu* Endler (1986:40:table 2.1).

2 Can we specify more the fitness concept, for instance, the dimensionality of this quantity ? As for these dimensions (we mean, the *types* of solutions to environmental problems), they will most of the time vary with the environment, and the relevant environment will most of the time vary with the biological study. Therefore, we cannot specify these dimensions here.

3 It is only fair to notice that casting the problem of fitness in terms of individual phenotypes instead of individual*'s* traits is not trivial, for any integration of the traits together into the individual would be lost. We are obliged to do this, however, since we describe here the gene-selectionist scheme.

4 Of course if a study deals with only one time-interval, not specifying the time-interval is tempting.

5 It will not escape reader's attention that fitness here is a phenotypic property and that it could be considered as part of the phenotype. The reason to keep the concept, is to help distinguishing between "raw" phenotypic properties, and those very phenotypic properties which are relevant for a given selectionist study. The same holds for the growth rate : it could be considered as part of the phenotype too. Here again, we artificially split the concept between phenotype, fitness and growth rate to help distinguishing the parts of the gene effects that "explain" the dynamics accross generations.

the rate of increase or decrease (in absolute or relative numbers), on a given time-interval, of the quantity of the causing gene. Increase or decrease result from replication and survival of the gene: a gene's phenotype is fitter, *i.e.* it solves better an environmental problem on a given time interval, if the gene increases in quantity on this time interval[1]. The rationale for tracking the gene's quantity is the bet that it will enable us to explain the phenotypes population dynamics[2].

For the moment, we only considered selective processes occurring during a single, complete generation[3]. What about longer trends of selection ? Notice that if the developmental environment varies across generations the same gene could have different phenotypes, displaying to selection hidden parts of its reaction norm[4]. This is typically the case with frequency-dependent development. To extrapolate, stochasticity let aside, unigenerational selective processes to multigenerational selective processes, we thus have to make the assumption that the developmental environment does not significantly vary, otherwise, we have to track its dynamics and to know the reaction norms. Of course if the selective environment (*sensu* Brandon 1992) varies we have to track it too. Only if the relevant developmental environment is held constant on the considered evolutionary time-scale, will the dynamics of the phenotypes population follow the genes population dynamics ; and only if the genotype-phenotype map is known, will the genes population dynamics explain the phenotypes population dynamics – which is, we assume, our primary *explanandum* (Lewontin 1974).

2.4 A note on maps

If the time-intervals used to define each map (geno-pheno and pheno-fitness) are identical (and they should be, as we shall see), we can concatenate the genotype-phenotype and the phenotype-fitness maps into a single genotype-fitness map: knowing $p=o(g, E_o)$ and $w=s(p, E_s)$ we can write $w=s(o(g, E_o), E_s)=\sigma(g, E_{o,s})$ where *o* is the geno-

1 Here we depart from the measure of fitness *sensu* Endler (1986:40:table 2.1): fitness is "measured by the average contribution to the breeding population by a phenotype, or a class of phenotypes, relative to the contributions of other phenotypes.". This stems from our concept of phenotype, which is attributed to a gene: *p=o(g,E)*. (Of course two genes can have the same phenotype.)

On the other hand, our approach is compatible, in our view, with Lehman's models (2007, 2009) on posthumous phenotypes. In these models, we would consider that the environmental problem to solve involves intergenerational processes (see 3.10).

2 This account supposes that each gene has approximately the same *per capita* impact on the world, or at least that the impacts have no geometrical dynamics. It could be the case that some genes have exponentially growing impacts without any replication nor survival of the gene, for instance, if their phenotype "grows" which is the case in particular if the phenotype is a replicator (Brown *et al.* 2008). In this case the fitness *sensu* "replication + survival of the gene" is insufficient to describe the phenotypes dynamics. In his thesis, Riboli-Sasco (2010) has explored the explanatory importance of the ratio between the *per capita* impact and the number of replicators.

3 That is, phenotypic selection *sensu* Endler (1986:12).

4 It is important not to get distracted by selection on developmental plasticity here. "Plasticity" is a kind of phenotype for which the developmental environment can be considered as constant even if the resulting trait varies (accordingly to the some environmental features) : the trait "plasticity" is constant, the resulting trait varies.

pheno map, s is the pheno-fitness map, σ the geno-fitness map, and E_i the relevant environment for process i (*i.e.* ontogenesis and/or selection)[1]. For the rest of the argument, we will suppose that such a concatenated map is defined[2].

The two maps (geno-pheno and pheno-fitness) or the single concatenated genotype-fitness map are *invariants* in our evolutionary explanations (the geno-pheno map is also an invariant in developmental explanations). Their dimensions include *variable* conditions, typically environmental ones, that allow to explain given cases[3]. These maps are defined with regard to given time-intervals (when the time-intervals tend to zero we talk about instantaneous phenotype and instantaneous fitness). Moreover, it is assumed that development and evolution are first order Markov processes (Lewontin 1983:279). Thus the instantaneous fitness of an instantaneous phenotype depends on the *current* state of the system, and in particular, possibly on the state of the phenotypes population (this is even more obvious for fitness differences). As the phenotypes population and the rest of the environment can vary through time, instantaneous fitness *and* instantaneous phenotype of a given gene are usually not invariant under translations in time. Only the maps are.

2.5 A note on spatial extension

Recall that we want to attribute environmental modifications to given genes (or replicators). Intuitively, we make the assumption that the further the spatial extension, the more the dilution of a gene's effect. And the more the dilution, the less the effect is expected to be relevant (beyond a given limit, we assume that the gene has a null effect). Moreover, *ceteris paribus*, the further the extension, the slower the selective feedback ; and the slower the feedback, the less the temporal covariance between selective events and the original gene (*i.e.* the less the effect on fitness). In this respect, physical boundaries do matter : because they avoid dilution of phenotypic effects. Noteworthily, “positive” phenotypic effects tend to be bounded, whereas “negative” (such as waste) tend not to be.

This invites our intuition to separate temporally the phenotypic effects extending beyond a given scale, from those extending above (typically the scale is given by the organism's boundary), and to consider those extending too far as both too weak and too slow to matter on

1 On experimental determination of these maps using RNA as a biological model, see Schuster *et* al. 1994, Huynen *et al.* 1996, Reidys *et al.* 1997.

2 This concatenation assumes that the maps are not mere correlations, for correlations are not transitive (see section 3.2). The concatenation can only be made assuming *ceteris paribus* conditions with respect to the environments of genes. For instance, if a gene is rather rare and always associated with a lethal gene, it will have a low fitness even if its “phenotype” is, otherwise, invaluable. To concatenate the maps, we have to assume that this kind of associations are negligible.

3 One more time, because we distinguished earlier between the genotype and the phenotype, we did not consider replication, survival, etc, in brief, evolutionary events, as phenotypes but as parts of the genes' evolutionary dynamics. However, there is nothing conceptually wrong considering death and reproduction as developmental events. But, we assumed a time-scale separation to distinguish between developmental processes and evolutionary processes. This forces us in turn to consider a separation between developmental and selective environments : the parts of the environment that influence the phenotype are developmental, and the parts that lead to selective events (death etc) belongs to the selective environment. These distinctions are more than widespread, but explaining their contingency is more than welcome.

our time-scale of interest. This is reinforced by the desire to separate developmental and evolutionary time-scales : considering too slow phenotypic effects would not allow it.
Our argument, here, is that spatial extension in itself is not what primarily matters : what matters is the time-scale separation between phenotypic effects that we judge relevant, and those that we do not. Of course, “relevance” depends on the case of study.

2.6 Concluding discussion on the selectionist scheme

The necessary invariance

As any explanatory device, the selectionist scheme relies on an unavoidable separation between an invariant, and a set of states. The separation between the invariant and the variables, in dynamical systems, relies on an implicit time-scale separation between the dynamics of the invariant (supposed to be close to zero on the considered time-scale) and the dynamics of the variables. In the selectionist scheme, we deal with several separations.

Time-scale separations

First, we separate hereditary (long lasting) from non-hereditary (short lasting) entities. We showed that this entails to assume non-(genetic)-inheritance[1] of acquired characteristics. The dynamics of an individual hereditary entity (typically a germline gene sequence[2]) is supposed to be invariant with regard to the dynamics of the surrounding world (let aside cases where the environment is mutagenic). From this separation stems the distinction between the phenotype, and the genotype that causes, *ceteris paribus,* the phenotype in the surrounding world.
From this geno/pheno distinction stems another distinction, the distinction between development and evolution. Indeed, though replication (in the broadest sense) is an effect of a gene on its environment and could thus be considered as a phenotype, we will typically not consider gene copies as part of a parental gene's phenotype (which would be still *developing* after the parent's death), but as part of an *evolving* genotypic lineage. Development is the dynamics of a single phenotype. Selection is the geometrical dynamics of genotypic lineage(s). Besides, because phenotypes are assumed not to replicate[3], they are not included in the bookkeeping of evolution. Only genes are units of bookkeeping.
From the distinction between development and evolution, it is tempting to posit a time-scale separation between developmental, and evolutionary processes. This time-scale separation is *not* embedded in the conceptual distinction between development and evolution. When separated, developmental and evolutionary processes would be the scope of respectively short term and long term explanations. This temptation comes partly from the geometrically growing explanatory power of geometrical dynamics with time, which promotes long-term

1 Or, more exactly, non-long lasting-inheritance. The question then is how much we can segregate between long and short lasting inheritance.
2 The evoked dynamics of an individual gene sequence can be considered as the ontogenesis *of the gene* (and not of the phenotype).
3 If phenotypes replicate, the selectionist will consider them as replicators, and will look for... their phenotypes (see *e.g.* Dawkins 2004). See our brief discussion of this case in section 5.2.

explanations, partly from the supposition that development lasts only one generation, and partly from the possibility to consider long lasting, faithfully replicating, hereditary entities.

Positing a time-scale separation entails that individual phenotypic dynamics will be invariant with regard to evolutionary dynamics of genotypic lineages and vice versa. In other terms, ontogenesis can be considered as instantaneous at the evolutionary time-scale and evolution can be considered as null at the ontogenesis time-scale[1]. Interestingly, a similar time-scale separation is also usually assumed between ecology and evolution (discussed in OLF 2003:231-235).

The simplest case of selection happens when the relevant developmental environment does not vary on an evolutionary time-scale (*i.e.* that if it varies, it can be averaged), such that the portion of the reaction-norm exposed to selection remains approximately constant on the long-term. Then, the geno-pheno map is more precise (*i.e.* more averaged!), linking a given genotype to fewer phenotypes than it would if the developmental environment should vary. Thus, the geno-pheno invariant is more stringent. If, in addition, the selective environment is invariant, then the fitness of a given gene is invariant under translations in time. In the most general case however, the fitness of a gene (even absolute fitness) is not invariant under translation in time.

There are no organisms in this scheme. Organisms do not faithfully replicate on the long term, thus they are not units of bookkeeping. Neither are they, because of sex in the most general sense, units of phenotype. Whatever their functional integration, they are let aside. This has, among other connotations, an important implication : the “environments” considered in this scheme are environments of genes, not of organisms ; phenotypes are always *environmental* modifications.

In summary, the selectionist scheme relies on the following invariants : the genotypic invariance (the long lasting hereditary entities), the genotype-phenotype map (the developmental rules), the phenotype-fitness map (the selective rules). It can include, or not, some invariant environmental features, in particular developmental or selective ones. As for the state of the evolutionary system, it includes the current population of genes (or other replicators), the current population of phenotypes, and the current fitness of each phenotype. It can include, or not, some variable environmental features (developmental or selective). Moreover, the selectionist scheme classically contains an additional assumption : that ontogenesis is time-separable from selection.

Externalism and internalism

Such a dichotomy between ontogeny and selection in the selectionist scheme has already been noticed by Lewontin (1983:274), though in somewhat different terms : “The essence of Darwin's account of evolution was the separation of causes of *ontogenetic* variation, as coming from internal factors, and causes of phylogenetic variation, as being imposed from the external environment by way of internal selection.”. Subsequently, the selectionist scheme has been described as *externalist* (Godfrey-Smith 1998:142). In our view though, the dichotomy has to be set primarily in terms of time-scale separations, which may in turn entail (or not)

1 This time-scale separation does *not* imply that the developmental environment is constant on the evolutionary time-scale, for ontogenesis could still be considered as instantaneous in the case of a variable developmental environment on the evolutionary time scale.

some space-separations of the variables. (See section 4.2 for a discussion of externalism in evolutionary biology.)

Historical roots and leafs

Interestingly, all the distinctions we listed above can be anachronistically traced back to Darwin (1859), stemming from its original scheme – let aside the pangenesis, which is "at total variance" with the scheme (Lewontin 1983:274, but see Jablonka and Lamb 2005:15), and the fact that organisms were central to Darwin (Lennox 2010, Huneman 2010). The original scheme was a long-term explanatory scheme, dealing with "an almost infinite number of generations" as for both inheritance (Darwin 1859:466), and accumulation of variations through selection (Darwin 1859:481). In practice though, biological systems are far from infinite. So what does "long term" precisely mean here ? Is there any term long enough to enable the evoked time-scale separations ? What is the scope of the selectionist scheme ? Precisely these are the questions that the "constructionists" ask.

3. What niche construction is

In this section we will expose what the niche construction processes are, and why the constructionists (Lewontin, Odling-Smee, Laland, Feldman and others) want to take them into account in evolutionary biology. We will have to specify some of the various meanings of niche construction. Then, we will examine the theoretical consequences of the niche construction processes, and in particular the relationship between the obtained niche construction theory and the selectionist scheme exposed above[1].

3.1 Construction in living systems

Examples

We cannot expose the rationale for niche construction better than OLF (2003:1) did in the first paragraph of their book :

"Organisms play two roles in evolution. The first consists of carrying genes, organisms survive and reproduce according to chance and natural selection pressures in their environments. This role is the basis for most evolutionary theory (...). However, organisms also interact with environments, take energy and resources from environments make micro- and macrohabitat choices (…), constructs artifacts, emit detritus and die in environments, and by doing all these things, modify at least some of the natural selection pressures present in their own, and in each other's, local environments. This second role for phenotypes in evolution is not well described (…) by evolutionary biologists (…). We call it "niche construction" (Odling-Smee 1988)."

This presentation has been repeated without substantive modifications in other papers of the team (*e.g.* Laland *et al.* 2003:117, Day *et al.* 2003:84, Laland 2004:316, Laland & Sterelny 2006:1751), we can thus take it for representative of the framework.

1 The niche construction theory is often called "extended evolutionary theory" and the selectionist scheme "standard evolutionary theory" by OLF (2003).

Definitions

The "niche" here is defined as "the sum of all the natural selection pressures to which the population is exposed" ; while "niche construction" is defined as "the process whereby organisms (...) modify their own and/or each other's niche" (OLF 2003:419), that is, the selection pressures to which their or others' populations are exposed. Please note that this is a particular meaning in the family of concepts reviewed in the first chapter of this thesis.
Definitions have to end somewhere, and "selection pressures" is let undefined. This is because OLF give a "glossary of new terms" (2003:419), not of old ones, but this is somewhat unfortunate because one major theme of their book is precisely to compare the old and new theories (OLF 2003:Chap.10). It will turn out that this very phrase of "selection pressures", bearing all its colloquial and lax meanings, is central to the claim (in the title of the book!) that niche construction is the neglected process in evolution.

Generalisation : niche interaction

Actually, niche construction does not deal only with evolution. Rather, the key is the rejection of the dichotomy between processes that are internal *vs* external to the organism (Laland *et al.* 2003:117), and consequently the rejection of externalism (especially, of course, in evolution).
Sometimes, niche construction has been understood simply as any modification of the environment (*e.g.* Laland *et al.* 1999:10242). Elsewhere, though, this meaning has been explicitly rejected, and niche construction has been defined as, rather, the "organism-driven (...) modification of the relationship between an organism and its relative niche" (Laland *et al.* 2006:1751, see also Odling-Smee 1988:89-100). In this respect, constructionists put a special emphasis on the *interactions* between organisms and their environments and would be better called interactionists[1].
This interactionist view explicitly traces back to Lewontin (1983:282). Lewontin proposes to characterize adaptationism (any other externalist explanation of an organism's dynamics would fit this characterization) as a pair of differential equations "describing the changes in organisms O as a function of organism and environment E (…) and the autonomous change of environment". He gets :

$$\frac{dO}{dt}=f(O,E)$$

$$\frac{dE}{dt}=g(E)$$

By contrast, he proposes the constructionist view in which organisms and environments are "each a function of the other" :

$$\frac{dO}{dt}=f(O,E)$$

$$\frac{dE}{dt}=g(O,E)$$

These metaphorical equations are repeated by constructionists as a banner for their view (*e.g.* Odling-Smee 1988:76, OLF 2003:16-19). We will come back to these equations in section 4.2

1 Indeed, they aim at subsuming niche construction (organism-driven modification) and natural selection (environment driven modification) into a single theory of the organism-environment relationship.

(see also section 6).

Before discussing the importance of niche construction in evolutionary theory, we have to discuss the many scales and meanings of niche construction. This will give the opportunity to question the formulation of the theory in terms of organisms, rather than genes.

3.2 The (non-)universality of construction

The thermodynamic (dis)proof

First, OLF deduce the universality of niche construction from a thermodynamic observation :

“A basic feature of living organisms is that they take in and assimilate materials for growth and maintenance and eliminate or excrete waste products. It follows that, merely by existing, organisms must change their local environments to some degree. Niche construction is not the exclusive prerogative of large populations, keystone species, or clever animals ; *it is a fact of life*.” (OLF 2003:36, my emphasis)

Farther, they are more precise :

“In the language of thermodynamics, organisms are open, dissipative systems that can only maintain their far-from-equilibrium states relative to their environments by constantly exchanging energy and matter with their local environments. (...) Two-ways interactions (...) do permit organisms to stay alive without violating the second law [of thermodynamics, A/N]. These two-way interactions account for the origins of obligate niche construction.” (2003:168). Again : “Niche construction is connected to thermodynamics by the fact that it *is* work.” (Laland *et al* 2005:49, their emphasis). The argument here is quite strange because there is probably nothing (or almost nothing) easier than finding externalist models of open dissipative systems. The key is, indeed, to delineate the relevant open system (see section 4.2).

Though, they temperate their claim : “Sometimes no practical consequences of any kind arise from these interactions with the environment and they can safely be ignored” (2003:169, see also *e.g.* 2003:8). But note that this is at variance with their previous (and repeated) claim that niche construction is an “obligate” “fact of life”.

Now, we are properly armed to rephrase OLF's claim and compare it with the “standard” view : OLF claim that the effects of the organisms on the environment cannot be time-separated from the effects of the environment on the organism ; thus, they co-evolve in the broadest sense. This is far from a trivial claim. The standard view would be the opposite : that the environment is big enough, and organisms' effects diluted enough, to neglect them on our usual time-scales. Actually, this is an empirical question. We cannot prove or disprove niche construction, reject or accept externalism, only by general considerations on thermodynamics[1].

1 Interestingly, Sterelny (2005) uses thermodynamical arguments for a different issue : that is, showing that barriers do matter in life : “Every organism is a system far from thermodynamic equilibrium, and is maintained at its far-from-equilibrium condition only by the expenditure of energy and by a barrier to the free flow of energy and material from the organism to the environment.”.

Here the argument is quite strange, because there seems to be an infinity of (self-)organized, far-from-equilibrium, systems which do not exhibit any obvious barrier to the flow : convection cells, Belousov-Zhabotinsky reactions, running sand dunes (Andreotti *et al*. 2002), to name just a few. Certainly, they

To make this central point clear, a comparison can be useful here. All living systems have some mass. Thus, by their growth, movements, etc, they must influence the gravitational field of Earth in some way. Gravitational construction is a fact of life. However, we do not take gravitational construction into account to compute the trajectory of Earth. This is because we implicitly posit a (time-)scale separation between the two processes: the effects of life on gravitational fields are (for the moment) so small that it would take them more than the solar system's life-time to be significant for us. This comparison shows how a time-scale separation can break a *possible* symmetry between two processes.

The correlation-propagation (dis)proof

One paper (Laland & Sterelny 2006:1757) contains another argument aiming at "deducing" the universality of niche construction from already known facts. It is worth discussing too, because it contains an attractive flaw:

"If there were no correlation between niche-constructing activities and environmental states, there could be no extended phenotypes. If there were no correlation between those environmental states that are sources of selection and (recipient) genes, there would be no directional selection. Provided niche-constructing by-products are consistently generated, modify selection pressures, and precipitate a genetic response, niche changing will be correlated with, and prior to, genetic change."[1]

Though intuitive, this argument does not withstand scrutiny (here we will focus on the two first sentences, the third is, strictly speaking, logically decoupled, and we give it here only to enlighten their point). The reason is that, despite intuition, correlations are not transitive (*sensu* transitivity of binary relations). If *A* is correlated to *B*, and *B* to *C*, this does not imply any correlation between *A* and *C*. Even if *A* is *positively* (resp. negatively) correlated to *B*, and *B positively* (resp. negatively) correlated to *C*, is not implied any correlation between *A* and *C*: they can be positively, negatively, or un-correlated[2]. For instance, there is a positive

seem less organized than the simplest organisms – granted an intuitive metrics of organization, which is far from obtained (but see the attempt by Bailly & Longo 2009). But this does not entail that effects extending outside the organism's barrier cannot be somewhat organized.

1 This argument is found also in OLF (2003:8) : "It is difficult to see how organisms can avoid doing this [modifying their own, and others' selective environments, A/N]. Environmental change modifies natural selection pressures (Endler 1986), while organisms are a known source of environmental change in ecology (Jones *et al.* 1997)." This time, OLF immediately give an amendment : "However, in order for niche construction to be a significant evolutionary process, it is not sufficient for niche-constructing organisms to modify one or more natural selection pressures in their local environments temporarily, because whatever selection pressures they do modify must also persist in their modified form for long enough, and with enough local consistency, to be able to have an evolutionary effect." This amendment is discussed later.

2 The reasoning is more obvious when considering long or infinite chains of correlations, for instance: A corr. to B, B corr. to C, C corr. to D, etc... Y corr. to Z. We would not bet on the positivity, negativity, or absence, of any correlation between A and Z.

The intuition of transitivity comes from the fact that in everyday life, correlations appear to be transitive "most of the time". Sometimes, it is possible to derive obligate transitivity for some sets of correlations, depending on the strengh of the correlations and the number of samples for each correlation. As for the strength, the limiting case is when $R^2=1$ for each correlation, where correlations are all transitive. The number of samples is important to be known, when the number differs from one correlation (*e.g. A* to *B*) correlation between youth and life expectancy, and a positive correlation between life expectancy and IQ (*e.g.* Whalley & Deary 2001), but there seems to be hardly any positive correlation between youth and IQ (we suppose our readers are adults).

In Laland & Sterelny's argument above, it may well be the case that the parts of the environmental states that are modified by the organisms are not sources of selection[1]. It is, besides, precisely the externalist claim. Yet all the correlations evoked in their argument hold.

3.3 The many scales of niche construction: development, ecology, (micro and macro) evolution

The same line of reasoning holds for thermodynamics and for development, ecology, evolution etc. Niche construction is the non-negligible modification by a living system of the environment acting on it, in such a way that there is a rough symmetry, *i.e.* an interplay, between their dynamics (on a given time-scale)[2]. Thus, developmental niche construction can be defined as the non-negligible modification by an organism (or a litter of siblings) of its developmental environment, ecological niche construction as the non-negligible modification by an organism (or a group/population) of its ecological environment, and evolutionary niche construction as the non-negligible modification by an organism (or a clone/species) of its selective environment.

In this paper, we will treat only evolutionary niche construction in details. Parallel accounts would hold for other scales of reasoning. Besides, it is important to notice that niche construction at one scale, does not imply niche construction at another scale. Thus, even if we had a perfectly interactionist model of the exchanges of matter and energy between an organism and its environment on a given thermodynamic scale, this would not imply that the organism modifies the local (or global) selection pressures on a given evolutionary time scale[3].

3.4 The many meanings of niche construction

Probably because of the programmatic nature of the niche construction framework (*e.g.* OLF 2003:304, Laland *et al.* 2005:53), the niche construction concept is protean, having many avatars with regard to the local questions. In addition to classifications according to the scales of study (mostly ecological *vs* evolutionary niche construction, OLF 2003:40,194), several dichotomies have been proposed

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and another (*B* to *C*): for instance, if *B-to-C* has few samples compared to *A-to-B*, it could be the case that all the samples of *B-to-C* are outsiders of *A-to-B*. Thus these correlations would not be transitive even if each is very strong and has relatively few outsiders.

1 We will specify later what “sources of selection” can mean (section 4.2).

2 Here we gloss over the desire of OLF to be inclusive and include modifications of *others'* environment. If there is no feedback on the focal living system on the considered time-scale, there is no symmetry between the living system and its environment.

3 We are indebted to Johannes Martens for having drawn our attention to this point. Here we gloss over perfectly closed organism-environment systems, which would remain perfectly closed at all scales.

OLF's dichotomies

OLF themselves distinguish :

(1) relocational *vs* perturbational niche construction, depending on whether the organisms move in, or physically change, their environment,
(2) inceptive *vs* counteractive niche construction, depending on whether organisms introduce change or neutralize autonomous change in the environment,
(3) positive *vs* negative niche construction, depending on the average effect on fitness (Okasha 2005 points to the fact that here, it must be specified whether the effect is on absolute or relative fitness)

(see OLF 2003:47 for a presentation of these concepts and 419-420 for the definitions).

The degree of selection : mere effects *vs* adaptations

Sterelny (2005) proposes in addition to distinguish between:

(4) individual and collective niche construction, and closely links this distinction to a dichotomy between:
(5) adaptation and mere effects.

Indeed, in Sterelny's view individual niche constructing effects can be selected for (or against), eventually leading to adaptations, while collective effects, though of tantamount biological relevance, cannot be selected because of a lack of covariation between the activity and the selection feedback at the individual level. Actually, there is more than a continuum between individual and collective effects (a continuum already noticed by Laland *et al.* 2005:39) and the individual/collective dichotomy does not directly relate to evolutionary effects. We will thus rather speak in terms of degree of selection (on, once again, a given time-scale), directly stemming from the rate of the selective feedback at the individual level. Dawkins (2004) makes a similar point, distinguishing niche change (*i.e.* mere effects) from niche construction (*i.e.* extended phenotype, in his view), for similar concerns about the covariation between a niche constructing activity, and a benefit in fitness. The distinction between adaptation and effects can be traced back to Williams (1966:3) and, as always, to Darwin (1859:46). It turns out to be of primary relevance to disentangle OLF's claims, frequently slipping between individual and collective levels (Sterelny 2005).

It is only fair to mention Laland *et al.* (2005) reaction to Sterelny's (or Dawkins', or Williams') distinction between adaptations and effects : “[T]here may well be a useful qualitative distinction between niche-constructing adaptations and effects, but the latter are every bit as consequential as the former. We strongly dispute any suggestion that only the former category matters in evolution. » (:51), “One of our major points is that certain important forms of feedback in evolution are consistently neglected because the conventional perspective discourages their consideration. (…) Sterelny’s use of the adjective ‘‘mere’’ to describe ‘‘effects’’ is common within evolutionary biology, and a good illustration of the current habit of dismissing the feedback from effects as inconsequential.” (:41). We will examine later how effects can be included in evolutionary analysis despite their tendency to escape direct selection.

Auto *vs* allo-niche construction (or narrow *vs* broad sense)

Finally, there is a last dichotomy that will be useful in our discussion : the distinction between living systems changing their own *vs* others' environments. This dichotomy is implicit in OLF's definition of niche construction (2003:419, quoted above). We propose the terms of, respectively, auto-niche construction *vs* allo-niche construction. In this vein, Okasha (2005:4) proposes to distinguish construction in the narrow sense (modification of ones' own environment) *vs* in the broad sense (including modification of others' environment), but this terminology is a little too neutral and can be misleading (for instance, it has already been used in a different sense by Godfrey-Smith 1998:148). According to Okasha (2005:2), the language of "construction" applies when living systems modify their own environment. This is at variance however with OLF's (2003:371) appeal to Godfrey-Smith's (1996:51,131) meaning of construction (section 1.2). There is a subtle tempting slippage here. An environment being defined with respect to a living system, when we talk about an organism modifying its environment, we intuitively expect that this will lead to some feedback on the organism itself (on a given scale of time), though the idea of feedback is not embedded in Godfrey-Smith terminology[1].

Laland *et al*. (2005:38) suggest that the terminology should not be given too much importance, and that if construction is not the appropriate term, then we should change the term rather than the argument. But words matter : some of their arguments precisely rely on slippages in their terminology (see sections 4.1 & 4.2). In particular, their central claim that organism and environment "coevolve" (*e.g.* OLF 2003:50), or that there is a symmetry between natural selection and niche construction (*e.g.* OLF 2003:14, Laland *et al.* 2005:41, Laland *et al.* 2006:1751), in a word, that niche construction is a new theory (OLF 2003:370-385), cannot be understood in terms of allo-niche construction. For allo-niche construction is a fundamentally asymmetrical process : it is nothing more than classical, asymmetrical, natural selection, where the selection pressures undergone by a living system stem from environmental features that are modified by an other, independent, living system. In this view, Laland *et al.* 1999 seminal paper does not actually deal with niche construction, but with classical natural selection[2].

1 Godfrey-Smith counts as "literal construction of the environment" the fact that "organisms alter the external world as they interact with it" (referring to Lewontin 1983).

2 The model is as follows: we consider an isolated population of randomly mating, diploid individuals, defined at two diallelic loci (with alleles E and e for the first, and alleles A and a for the second). The relative fitness of A depends on the presence of a given resource R whose renewal rate depends on the frequency of E. If there is no linkage disequilibrium, the evolution of the frequency of A depends on an external source of selection (that is E, through its effects on R), and the evolution of E does not depend on its own "niche constructing" effects.

Laland *et al.* (1999) do not explore the situation with linkage disequilibrium, because it had already been addressed in Laland *et al.* 1996 (with a similar model). Unfortunately Laland *et al.* (1996) do not dwell on the dynamical implications of linkage. Thus, the claims on Laland *et al*. (1999) on the dynamical implications of niche construction (generating inertia and momentum) do not illustrate auto-niche construction. OLF (2003:chap. 3) sum up Laland *et al.* (1996, 1999).

Here are the genotypic fitnesses (Laland *et al*. 1999:table 1), where it can be seen that E's fitness does not depend on R, and thus that construction does not feed back on itself. α and β represent selection independent of R.

Though Laland *et al.* (2005:41) claim that "throughout our studies on niche construction we have been consistent in utilising the broad definition" (broad here *sensu* Okasha 2005, *i.e.* auto- and/or allo-niche construction in our terminology), we must confess that they were not. The central figure of their book for instance is cast in terms of organisms modifying *their own* environment, not others' (OLF 2003:14 fig.1.3, reproduced below).
For all these reasons, for the rest of the chapter we will restrict niche construction to auto-niche construction, where living systems modify their own environment (however, to save ink we will not specify "auto" every time)[1].

3.5 What the focal living system is (organisms *vs* genes)

Until now, we have been neutral with regard to the living systems in question and their relative environments (except cases where we borrowed others terminology, *i.e.* "organism", for clarity in discussing their quotes). This is because we mostly discussed niche construction in the general sense, not only evolutionary niche construction, and because the living system to consider depends on the considered type of construction. Now, we will specifically focus on evolutionary niche construction : the modification, by a living system, of the selection pressures acting on it. It is time to reap the fruits of our discussion of the object of selection (section 2.2 & 2.3).
One striking aspect of niche construction theory is the discrepancy between the verbal accounts of the theory, framed in terms of *organisms*[2] both transmitting their genes and modifying their environments (*e.g.* OLF 2003:1, 14:fig.1.3), and the mathematical models of the theory, framed in terms of *genes* having phenotypes (OLF 2003:387-410), or, for cultural evolution, in terms of phenogenotypes[3] (OLF 2003:411-418). Laland (2004:324) himself, in a programmatic conclusion, oscillates: "In my terms, there are two processes in evolution, natural selection and niche construction. There is a power and utility to regarding the gene as the unit of selection, but equally there is value to seeing the organism as the unit of niche construction."

	EE	*Ee*	*ee*
AA	$\alpha_1\alpha_2 + \varepsilon R$	$\alpha_2 + \varepsilon R$	$\beta_1\alpha_2 + \varepsilon R$
Aa	$\alpha_1 + \varepsilon\sqrt{(R(1-R))}$	$1+ \varepsilon\sqrt{(R(1-R))}$	$\beta_1 + \varepsilon\sqrt{(R(1-R))}$
aa	$\alpha_1\beta_2 + \varepsilon(1-R)$	$\beta_2 + \varepsilon(1-R)$	$\beta_1\beta_2 + \varepsilon(1-R)$

As for the dynamics of the resource, it is of the type: $R_t = f(R_{t-1},p_{E\,t})$, where p_E is the frequency of *E.*

1 It is hard for us to make sense of the following argument, so in order not to ignore it we give it to the reader : "Third, Okasha claims that ''some of OLF's own arguments seem to presuppose the narrower rather than the broader notion of niche-construction'', suggesting that our perturbation-relocation and inceptive-counteractive dichotomies only makes sense relative to the constructor. We think a more useful distinction here is between 'phenotype' and 'extended phenotype' (Dawkins 1982). The constructing activity (phenotype) can be described as perturbatory or relocatory, inceptive or counter-active, but the change in the environment (extended phenotype) cannot. To the extent that other organisms typically experience the change rather than the act of changing then, as Okasha says, these sub-categories of niche construction do not pertain to the modified environment of other organisms. However, neither do they relate to the modified environment of the constructor. The distinction is between constructing and construction, not between feedback to self or other." (Laland *et al* 2005:40)

2 The verbal theory is framed in terms of organisms, but with the notable exception of the discussion of EMGAs (environmentally mediated genotypic associations) for ecological studies (OLF 2003:217-224)

3 Phenogenotype: specified combination of a genotype and a variant for a cultural trait (OLF 2003:420)

This discrepancy traces back to Lewontin (1983) and comes from the underlying interactionist view of biology, which does not favor qualitative or causal separations between involved living entities: “Genes, organisms, and environments are in reciprocal interaction with each other in such a way that each is both cause and effect in a quite complex, although perfectly analyzable, way.” (1983:276).
Even when putting the standard evolutionary view in a nutshell, Lewontin himself oscillates: first, he sketches adaptationism in terms of organisms “The organism proposes; the environment disposes.” (1983:276), and traces this view back to Darwin (Lewontin 1983:273). This is at variance with Williams' (1966) and Dawkins' (1976) gene-centred views, which could have been considered as the most classical externalist evolutionary perspectives at that time (by now, each clan claims to have won the war, see *e.g.* Dawkins 1976-2006:xv and Mayr & Provine 1998:xiii). But farther, Lewontin changes his tune: “Norms of reaction cross each other so that no genotype gives a phenotype unconditionally larger, smaller, faster, slower, more or less different than another. These well-known facts seem, however, to have made no impact on evolutionary theorists who continue to speak about selection for a character and about genes that are selected because they produce that character.” (1983:278). Thus he criticizes the mainstream theorists for being gene-centrists.
Then he proposes his own interactionist view: “Organisms do not adapt to their environments: they construct them out of the bits and pieces of the external world.” (1983:280). And this view is again framed in terms of organisms (this quote is repeated in OLF 2003:17, see also the pair of differential equations given above).
Words matter. Semantic slippages are the brownian motion giving rise to philosophical heat. (For scientific heat, we enjoy in addition slippages in the interpretation of models' parameters.) If Lewontin (and followers) opposes to the externalism of classical gene-centrism by arguing the interactionism of an organism-centered view, the two views are very likely to talk past each other. Not the same environments, not the same invariants, are discussed.
Indeed, if Lewontin and followers are right, that is, if uncoupling organism and environment is illicit on (for instance) the evolutionary time scale, there is still a way to rescue externalism: that is to consider that the organism/environment pair is not the right couple to consider for evolutionary studies. Two declinations of this idea have already been explored, one shrinking the organism, the other extending it.
The first one, that we exposed at some length in section 2.2, is to consider that the units of selection are not organisms but genes (*sensu* nucleic acids), both because genes are supposed to be units of replication, and because it is supposed possible to determine a relevant average phenotypic effect of a gene, giving rise to selection (Dawkins 1976, 1982). Here, modifications of the (intra or extra organism) environment are gene's (always extended) phenotype.
The second one, is to consider that the boundary we draw around an organism is somehow arbitrary, and that, for instance, “the edifices constructed by animals are properly external organs of physiology” belonging to an “extended organism” (Turner 2000:ix). Here, modifications of the environment are organism's extended phenotype. As we saw in section 2.2 & 2.3, framing the selectionist scheme in terms of organisms is complicated, because organisms (when identified) generally do not breed truly enough for our desired explanations

of intergenerational dynamics. Thus we will not explore the extended organism perspective here. The same arguments than those we will give would hold for organisms provided that they fulfill the requirements of the selectionist scheme.

For the above reasons, from then on we will discuss only *genetic* evolutionary (auto) niche construction[1] : that is, *the process whereby genes modify their own selection pressures*. We now have to clarify the notion of selection pressures.

3.6 What selection pressures are: variables or invariants?

The most explicit definition of selection pressure according to OLF is to be found in their discussion of the evolutionary niche (2003:40): “In principle, it would be possible to relate each selection-pressure dimension to a specific utilization distribution, such that the resource frequency corresponds to the intensity of selection that would be acting on the population.” Farther, in a caption (2003:49:fig 2.1) they seem to assume a selection pressure as “arising from an environmental factor”. Odling-Smee (2007) himself “provisionally assume[s] that these selection pressures are themselves derived from energy and matter resources in the environments of organisms.” These quotes deserve clarification (see also section 4.2).

More generally, we have found in the literature two classes of meanings of “selection pressure” with regard to the time-scale of the evolutionary explanation: (1) the local and (2) the global *explanans* of a dynamics (here local and global mean *in time*).

Selection pressures as local *explanans*

To the first class belongs the interpretation of selection pressures in terms of current selection coefficients (that is, differences in current fitness values) in population genetics or quantitative genetics, or selection gradient (that is, invasion fitness) in adaptive dynamics. (For uses in population genetics, see *e.g.* Staff 1977, Durham 1991:121 fig.3.4, Kimura 1994:288, Ehrentreich 2008:155, Stephens 2010:133. For uses in adaptive dynamics, see *e.g.* Clobert *et al.* 2001:76, 88, 138, 271.) When selection is frequency-dependent (which is the paradigmatic case in adaptive dynamics), current selection coefficients/gradients suffered by given genotypes vary through time accordingly to the population's composition, and they cannot provide robust insights on the selective dynamics at time-scales exceeding one (or not much more) generation. In this case it will be easier to think of them as *variables* of the dynamical system. Whenever selection is *not* frequency-dependent (which is the paradigmatic case in population genetics), selection coefficients are *invariant* under modifications of the population composition (and in particular, modifications of his composition through time) and can thus be said to belong to class (2) as well (below).

1 Here we tune OLF's definitions into genetic terms in accord with their mathematical models and restrict ourself to auto-niche construction *sensu* modification of selection pressures in accord with their big (verbal) theoretical view. Just the other perspective would be to consider organisms rather than genes, in accord with the big theoretical view, and niche construction *sensu* mere environmental modification, in accord with their mathematical models. The obtained theory would reduce to ecosystem engineering (Jones *et al* 1994).

Selection pressures as global *explanans*

To the class (2) belongs the interpretation of selection pressures in terms of long term invariants driving the long term (selection) dynamics of the population. This is well exemplified in the following quote by Sterelny (2005). Discussing frequency-dependent selection of sneak *vs* guard strategies in fishes populations, Sterelny writes: "More importantly, even if an agent's choice makes a difference to the local ratio, there is an important sense in which this does not change the selective environment. It does not change the equilibrium ratio of sneaks to guards. (…) On the assumption that evolutionary agents are individual organisms, the per capita effect of each agents action is typically not niche altering. It will not usually change the local ratio, and it will not change the equilibrium ratios that determine the long-run dynamics of the population." (See also *e.g.* Mayr 1988:409, Sober 2000:59, Grene and Depew 2004:272, Sober and Lewontin 2009:305, Cummins and Roth 2009:84 for other similar understandings.)

Selections pressures in niche construction

Note that the *explanandum* depends on the *explanans*. With local *explanans* (class 1), we focus on current, transient, aspects of the dynamics. With global *explanans* (class 2), we are more inclined to deal with steady states (possible ESSs[1], for instance). That Sterelny supposes that there will ever exist an equilibrium ratio of sneaks over guards is a good illustration. The two interpretations are compatible, in the sense that selection coefficients can vary through time (in the paradigmatic case of frequency-dependence) according to a long-term invariant, which would be in our case the pay-off matrix (which is frequency independent). But this is *not* the same to say that genes have an impact (say by construction) on the current pay-off they experience (which is the usual role for phenotypes) and to say that they modify the pay-off matrix (which is more unusual).

The clues given by OLF do not allow to decide between the two interpretations as for the selection pressures that should be modified by niche construction. In fact, we think they oscillate.

On the one hand there are some reasons for understanding niche construction as an avatar of frequency-dependence. For instance in the quote given above (OLF 2003:40), if selection pressures have to be understood as resource distribution, and phenotype as utilization distribution, and if the impact of utilization on the dynamics of the resource is significant (only) at the time-scale of one generation, we obtain classical frequency-dependence. Besides, OLF (*e.g.* 2003:120-121) consider frequency and density-dependence as cases of niche construction (following Lewontin 1983:282)[2].

On the other hand, when OLF argue for a symmetry between niche construction and natural selection in evolutionary dynamics (*e.g.* Laland *et al.* 2006:1751, OLF 2003:14:fig.1.3), they must imply that niche construction is the modification, by the selected living system, of the

1 ESS : evolutionarily stable strategy : "a strategy such that, if all the members of a population adopt it, then no mutant strategy could invade the population under the influence of natural selection" (Maynard Smith 1982:10)

2 However, OLF (2003:123) regret that models exploring frequency-dependence rarely consider the modification of fitness on other loci.

long term selective invariants (*e.g. t*he pay-off matrix in frequency-dependence). For, otherwise, there would be no such long term symmetry : natural selection would "win" on the long term (natural selection here *sensu* the invariant determining who, given a context, invades). And this long term symmetry between natural selection and niche construction seems dear to their heart, as they endlessly repeat that niche construction is not subservient to natural selection, that natural selection never preceded niche construction, even when we look back at the origins of life (*e.g.* OLF 2003:19). We will come back later to the issue of reciprocal causation (or cyclical causation) and symmetry between natural selection and niche construction.

For the moment, we have to remain neutral as for the meaning of selection pressure in OLF's writings. To avoid confusing the discussion, we will avoid this term whenever possible (except when discussing others' quotes). We will rather speak in terms of selection coefficients (possibly frequency-dependent) and of (implicitly long term) selective invariant (frequency independent)[1]. The selective invariant is invariant with respect to the phenotypes being selected[2] and can be treated as the phenotype-fitness map. This means that phenotypes are *variables* in the selective process[3].

Using our previous formalism, we can characterize selection pressures *sensu* selection coefficients *c(t)* as differences in fitness at time *t*:

$$c(t)=w_1(t)-w_2(t)=\sigma(p_{1,}E_\sigma(t))-\sigma(p_{2,}E_\sigma(t))$$

Assuming a genotype-phenotype mapping, we can transform the definition :

$$c(t)=\sigma(\mathrm{o}(g_{1,}E_\mathrm{o}(t)),E_\sigma(t))-\sigma(\mathrm{o}(g_{2,}E_\mathrm{o}(t)),E_\sigma(t))=\sigma(g_{1,}E(t))-\sigma(g_{2,}E(t))$$

Frequency-dependence is a special case where $E(t) = f(G(t))$, where G stands for the population of genes. Niche construction is a more general case where $E(t) = f(G(t'), t' \leq t)$.

A special case occurs when $E(t)$ is invariant, that is $E(t)=E$. In this case we can drop E in the selective invariant and write:

$$c=\sigma_E(g_1)-\sigma_E(g_2)$$

The selective invariant σ actually always depends on implicit environmental invariants (by writing σ_E ,we specify only one implicit environmental invariant here). Niche construction hypothesis is that such previously assumed environmental invariants are actually variables (see 3.10).

The shift of emphasis from genotypes (in population genetics colloquial meanings of selection pressures) to phenotypes (in our terminology) is more exact with regard to the selective process, and will turn out to be necessary to clarify what niche construction is (recall that we defined phenotypes as effects of genes on the world). Fitness and selective invariant are, as always, defined with respect to a given time-interval, but they are by construction defined *on*

1 Given the current population's distribution and the environmental state, the selective invariant determines the selection coefficients. The case where the selection coefficients are equal to the long term selective invariant is a limit case where these variables (the selection coefficients) are held constant throughout the selective process.

2 This means that whatever the phenotypic composition of the population, the selective invariant will remain the same.

3 A similar invariance holds for the developmental invariant, which is invariant with regard to the considered genes : genes are variables in the developmental process.

the same time-interval[1]. Moreover, the selective invariant is invariant through translations in time (in the extent of a given time-scale), while fitnesses and selective coefficients are not necessarily. We will discuss this notion of "time interval" at length later.

Selective environment and natural selection

Sometimes OLF use "selective environment" or "natural selection" (*e.g.* OLF 2003:19,376 quoted below) instead of "(natural) selection pressure". "Selective environment" and "natural selection" are not included in the definitions of the theory (2003:419), so to avoid endless exegeses we will provisionally consider them as synonyms (or misnomers) for "selection pressure". In section 4.2, we will come back to the notion of "pressures" stemming from the "environment". For the moment, the point with these terms remains the same, that is, the question of knowing whether OLF mean an invariant or a variable of the selectionist scheme, when they invoke selective environment or natural selection.

3.7 OLF's review of past theory

Before continuing the conceptual analysis of what niche construction can be, we must make a detour with a discussion of past theory. This discussion will help identify what is at stake concerning the novelty of the theory and its relationships with already existing theory.
OLF aknowledge that "In the ecology and evolution literatures there is a considerable body of formal theory that models aspects of niche construction and its consequences" (2003:117). They give several examples that they aim at interpreting as pre-niche construction studies (2003:117-133): resource depletion in ecology (we will not discuss it here, as it relates to *ecological* niche construction), frequency- and density-dependent selection (we just discussed the issue of frequency-dependence, roughly the same reasoning would hold for density-dependence), coevolution, habitat selection, maternal effects (see section 3.10), environmentally mediated epistasis (briefly discussed in section 5.5, it relates to *developmental* niche construction), gene-culture coevolution (to be discussed in future work), evolution in spatially heterogenous environments, and "other approaches" (listed below). In their view, these bodies of theories investigate some cases of niche construction but in a disparate and non-systematic manner (2003:132).
However, these examples are understandable within the "classical" selectionist scheme, as we have seen or will see. Words matter here, because if niche construction theory reduces to rephrasing classical theory into new terms, it cannot be said to be a new theory, only a cosmetic. However, we believe that niche construction theory contains intrinsic novelties that could account for relevant empirical facts (section 3.10).

Coevolution

OLF (2003:67-115) collate a large number of evolutionary cases of niche construction that fall into the categories of intra- or inter-genomic coevolution: "There is also a substantial body of circumstantial evidence that the niche construction of organisms has modified selection pressures and generated selection for alternative traits. This includes selection for

1 Time interval: that is, Δt or dt in dynamical systems.

anatomical and behavioral adaptations that enhance the efficiency of their niche construction, adaptations to relocation, selection favoring elaboration and regulation of the constructed resource, and selection for modified courtship, mating, and parental behavior. Although it is not clear that all of these adaptations are actually evolutionary responses to priori niche construction, it is likely that many of them are." (2003:112-113).

For instance, moles (*e.g. Talpa europea*) both dig burrows and display digging legs and poor eyesight (2003:77:table 2.3) ; fungus-growing termites build mound where "ventilation system of vertical channels in thick outer walls utilizes metabolic heat of fungus to power air conditioning and gas exchange" (2003:80:table.2.4) ; these termites also "cultivate fungi on which they are nutritionally dependent in specially constructed chambers" (2003:89:table2.5) ; some birds (*e.g. Sula dactylatra*) have vestigial, though elaborated, nests that function "as a courtship ritual promoting pair formation" (OLF 2003:98:table2.6). As for multispecies interactions, let's mention for instance, "in plants, the evolution of flowers and other adaptations for attracting insects and facilitating pollination" (2003:106:table2.7). (These examples are, in our view, representative of OLF's tables.)

Hence, any behavioral aspect of any living system should count as niche construction, even if they can be explained by the classical scheme, as soon as some part of the external environment (of the organism) is involved. Though we agree that an extended evolutionary theory should include classical natural selection as well as niche construction, we think that labelling any "external" behavior as a niche constructing one obscures the novelty of niche construction theory.

As for organisms adapting (or more neutrally, responding) to their own niche construction on the evolutionary time, Turner (2000) shows how external adaptations can be thought as external organs of an organism. Thus, OLF's examples will be more easily understood as intra-genomic coevolution[1], comparable to the evolution of physiological adjustments (if any) of classical organs. As for organisms responding to others' niche construction, Darwin himself already acknowledged the importance of the co-dependence of living systems : "I should premise that I use the term Struggle for Existence in a large and metaphorical sense, including dependence of one being on another." (1859:62, see also *e.g.* 3, 60, 75, 109, 132 ; for an extensive work on coevolution, see Darwin 1862).

OLF are perfectly aware that their examples involve coevolution (*e.g.* 2003:113, 124-125) but to them, coevolution is an instance of niche construction : "Models of coevolution of two or more species implicitly or explicitly take account of the fact that the niche construction of one population can affect the selection on another." (2003:124)

However, coevolution between species or between locus can be thought as frequency-dependent evolution (for interspecific frequency-dependent coevolution, see Seger 1992). As long as (we insist: as long as) there is no modification (*sensu* construction) of the pay-off matrix on the considered time scale, we have natural selection, not niche construction.

Intriguingly, this is not what scares OLF : "One possible criticism of our argument that niche construction plays a central role in evolution is that, in some of the examples we have given, genetic variation for the recipient trait may not have been present at the time the niche-constructing trait evolved, [thus] the traits [could not] be said to coevolve, and the evolution

1 Except, of course, cases where the extended organism contains several genomes, in which case the coevolutionary process would be inter-genomic.

of each trait could be treated separately." (2003:113). Well, the question they respond to here seems to be whether niche construction played the role of initial conditions (a role stressed by OLF elsewhere, though not in these terms, see section 5.3), or of a concomitant process. OLF respond to this criticism that empirical evidence makes it improbable that the traits did not effectively coevolve[1]. Unfortunately, this question relates to the relevance of taking coevolution into account, not directly to the relevance of revising the asymmetry between phenotypes and selection in the selectionist scheme.

This issue is of primary importance because of OLF's claim (e.g. 2003:290, see also Laland 2004:321, Laland et al. 2005:41, Laland & Sterelny 2005:1759, and section 4.1) that niche construction adds, in addition to classical natural selection, a second route to the adaptation of an organism to its environment, relies on cases of intra-genomic coevolution between "genes for" classical organs and "genes for" external organs (sensu Turner 2000). What OLF present as cases of organisms modifying their selection pressures can thus be reinterpreted, at first sight, as cases of coevolving genes, some of them having extended phenotypes[2]. We will discuss the issue of adaptation at some length in section 4.1.

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1 They also give two other responses (OLF 2003:113-114) : "niche construction can be dependent upon learning" without involving any genetic variation (we already discussed this point) ; "the consequences of niche are likely to be far more profound than just trait coevolution." (we will discuss this with regards to phenotypes extended in time). We do not mention these responses in the main text because they seem to us a little off topic with regards to the original criticism.

2 The reader might wonder why OLF limit niche construction to modifications of the external environment, and not of the internal environment : if most of niche construction is actually intra-genomic coevolution, why not considering also coevolution between genes having non-extended (*sensu* below organism's boundaries) phenotypes ? Actually, they do not limit niche construction to external modifications, as the quotes below show. For the time being however, the concept of "internal niche construction" is rather anecdotal in the literature, and seems to relate to developmental niche construction, not evolutionary niche construction of internal features. The underlying rationale of putting the emphasis on external modifications for evolutionary niche construction is, in our view, the intuition that external modifications can survive more easily the death of the agent. See also the discussion of the selectionist scheme as an externalism (section 4.2). Here are two illustrative quotes :

"Updating Waddington (1953), Schwenk and Wagner (2004) attempt to solve the paradox of developmental constraints by proposing that natural selection is resolvable into ''external'' and ''internal'' components. By external selection they mean the conventional sorting between variant organisms in populations. By internal natural selection they mean selection derived from the contemporary internal dynamics of a developing organism, that is, ''the characters interaction with other characters of a system within the internal milieu'' (p 395). (…) In theory, niche construction too is resolvable into external and internal components. Conceivably, it may be useful to consider the expression of transcription factors by genes in the internal environments of developing organisms as consistent with the logic of ''internal niche construction,'' whether or not this is the best label to use. " (Laland *et al*. 2008:559).

And :

"Is there anything in common between "internal niche construction" in developing organisms, and "external niche construction" by populations in ecosystems ?" (Odling-Smee 2009, in Barberousse *et al*. 2009)

Habitat selection

"Habitat selection refers to cases where individuals with a particular genotype are able to choose the habitat in which their fitness is greatest (Rosenzweig 1991). It is, therefore, a form of relocational niche construction (…)." (OLF 2003:123). Laland *et al.* (2007:53) go further : "… niche construction subsumes habitat selection, dispersal and migration."

Rather, we would consider that habitat selection is a case of intra-genomic coevolution and that invoking niche construction is superfluous (if not argued) : habitat selection that "channel[s] the direction of adaptive evolution" (OLF 2003:124) and subsequent (if any) adaptation to the chosen habitat are similar to other cases of coevolution where one locus channels another locus' evolution. Thus the account on coevolution given above holds.

By contrast, by counting habitat selection as a case of niche construction, OLF implicitly mean that there is a dynamical symmetry between habitat choice and selection by habitat. This symmetry is an empirical claim on the time-scales of the processes, that cannot be proven with mere verbal rephrasing.

Evolution in spatially heterogeneous environments

OLF (2003:129-130), following Holt and Gaines (1992) remark that in a spatially heterogeneous environment, "evolution can be channelled (…) toward adaptation to those regions of niche space in which abundance is greatest, rather than to other regions.". This is because a variant enhancing fitness in a patch or a niche with an initially higher abundance than in other patches has a selective advantage : if invaded, the patch will "water" the other patches by dispersal more than these patches will do. Holt and Gaines (1992) conclude that natural selection should be conservative with regards to the fundamental niche, where abundance is expected to be higher. The fact that demographical increase is favourable to selection was already present in Darwin (*e.g.* 1859:41), as well as the positive feedback between demographical increase (*i.e.* adaptability) and adaptation (*e.g.* 1859:125).

As regards niche construction, OLF (2003:130) point to the fact that "[i]f adaptation to a local environment increases population size there, then the importance of that environment relative to other local environments over the species distribution as a whole will be increased. One consequence of this is that niche construction in a particular local environment that leads to an increase in population size there automatically biases selection toward further adaptation in that environment (…)."

Ceteris paribus, the reasoning is indeed right, whatever niche construction means. It does not show, however, that we cannot understand this kind of facts within the classical selectionist scheme. Here, we can consider that positive niche construction is an adaptation like any other adaptation, and that, following Darwin, it enhances adaptability (here "positive" and "adaptation" are to be understood in terms of absolute fitness).

Other approaches

OLF (2003:130-132) cite three other previous approaches that seem close to niche construction : dynamic selective environments, *sensu* selection coefficients (OLF 2003:130) (*e.g.* Kimura 1954, Haldane and Jayakar 1963, Lewontin and Cohen 1969, Gillepsie 1973, Van Valen 1973, Karlin and Liberman 1974, OLF's citations[1]), feedback loops in evolution (Roberston 1991), and the extended phenotype (Dawkins 1982) (we will discuss this issue at length below). OLF argue that in previous approaches of dynamic selective environments, the dynamics were autonomous, not "respond[ing] to the activities of the organisms under study" (2003:131). This is at variance however with their position on coevolution as a case of niche construction (given above), because Van Valen's Red Queen principle (1973) states that "For an evolutionary system, continuing development is needed just in order to maintain its fitness relative to the systems it is coevolving with.". Robertson's approach, though elegantly abstract, is also based on coevolution (1991:470).

We thus have two kinds of previous approaches listed here (in addition to the extended phenotype, discussed right below) : autonomous dynamics of selection coefficient, and coevolution. The first is obviously classical, asymmetrical, natural selection. The second has already been discussed. None of them involve or imply niche construction, which pleads for theoretical novelty of the construction framework, if founded, but pleads against a particular foundation of niche construction in these approaches.

3.8 To build, or not to build?

Now that we have worked out the definition of niche construction and confronted it to past theory to specify what niche construction is not, we are going to tackle what is, in our view, truly new in niche construction. This novelty stems from a deep, intrinsic, thought-provocative, paradox nested in niche construction: in the selectionist scheme, modifications of the environment by a living system are usually thought as parts of its phenotype, not part of the selective process the living system undergoes: living systems are selected *according to* their phenotypes. There is a separation, thus, between the selection and the phenotype. In niche construction, there seems to be no such separation: genes modify the environment, and these modifications can be considered either as impacted by selection (as phenotypes) or as impact*ing* selection (as construction). This stems directly from OLF's definition of niche construction (2003:419, quoted above). Laland (2004:320) puts the paradox in a nutshell : "... some extended *phenotypes are 'heritable'*. Organisms not only acquire genes from their ancestors but also an ecological inheritance, *that is, a legacy of natural selection pressures that have been modified* by the niche construction of their genetic or ecological ancestors (Odling-Smee 1988)" (my emphasis). Thus, phenotypes have the status of selection pressures *on themselves*[2]!

The paradox is nested in the lax meaning of selection pressure. It is a paradox because at first sight, to make sense of any selectionist scheme, there must be an asymmetry between what selects and what *is* selected: the first seems to be a process (or an invariant function, in dynamical systems), the second seems to be a variable. Depending on the meaning of "selection pressure" (variable selection coefficient or selective invariant), this asymmetry

1 OLF also cite Hartl & Cook 1973, *Balanced polymorphism of quasineutral alleles*, Theoretical Population Biology, 4:163-172. We have not been able to find this paper, thus we do not cite it in the main text.

2 Or, to be precise, on (reiterations of) themselves later in time. We will examine later phenotypes extended in time. The reader might find the claim to be trivially true for frequency-dependence, but it is no longer trivially true if we do not limit its range to frequency-dependence. Here, we remain neutral as for frequency-dependence, not to trivialize *a priori* niche construction theory.

might seem to be relaxed by niche construction (it is relaxed when the former selective invariant becomes modifiable and thus, becomes a variable). Thus, on the one hand, OLF aim at integrating natural selection and niche construction into a unified extended evolutionary theory (OLF 2003:chap.10, Laland *et al.* 2005:53[1]). On the other hand, the theoretical extension precisely consists in relaxing the intrinsic asymmetry of selection by enabling genes (or organisms) to modify the "selection pressures" through their phenotypes.

We are going to discuss this issue at some length. It will appear deeply related to the relationship between niche construction and extended phenotype, that we discuss right below. Just after, we will discuss particular cases of extended phenotypes: that is, phenotypes extended in time, or posthumous phenotypes. This discussion will provide us with a re-definition of niche construction. In the following discussions, we will suppose that the phenotype-fitness map[2], that is, what we call the selective invariant, is never modified (remember that it contains environmental variables, such that the dynamics of the selective environment modifies only the current fitness, not the map). Niche construction theory will not necessarily vanish. We will then relax the assumption of invariance of the phenotype-fitness map, but this will not be for the good of niche construction: rather, natural selection will vanish.

Niche construction or extended phenotype?

As niche construction is (sometimes by definition: *e.g.* Laland *et al.* 1999:10242) living system driven environmental modifications, the immediate intuition is to think of them as extended phenotypes (Dawkins 1982), and thus to reduce niche construction to classical natural selection. Dawkins exemplifies such a reduction: "... niche construction ... confuses two very different impacts that organisms might have on their environments ... mere effects and engineering [of their] own environment[3]... Niche construction is a suitable name only for the second of these two (and it is a special case of the extended phenotype)." (2004:379).

Yet, the extended phenotype theory does not assume the modification of the selection pressures. Besides, it is gene-centred, not organism-centered as niche construction theory, but the organism is probably not the relevant unit here (sections 2.2, 2.3, 3.5, and 4.2). This point is acknowledged, though not conceded, by OLF (2003:131-132).

OLF take (great) pains to clarify that we should not perform such a reduction. To them, in contrast, "Dawkins' (1982) extended phenotype [is] one theoretical construct that captures

1 See *e.g.* Laland *et al.* (2005:53): "For example, it grants phenotypes a limited capacity to co-direct the genetic evolution of their populations by recruiting ontogenetic processes to modify natural selection. That raises philosophical issues that are more often associated with ''Lamarckism''. However, niche construction is not Lamarckian, It is Darwinian. It only modifies orthodox Darwinian selection."

2 As well as the genotype-phenotype map, which is not in question here (it concerns developmental niche construction).

3 This quote actually contains a quote of Sterelny that we cut for clarity of the main text. Here is the entire quote : "The problem I have with niche construction is that it confuses two very different impacts that organisms might have on their environments. As Sterelny (2000) put it, *Some of these impacts are mere effects; they are byproducts of the organisms's way of life. But sometimes we should see the impact of organism on environment as the organism engineering its own environment: the environment is altered in ways that are adaptive for the engineering organism.* Niche construction is a suitable name only for the second of these two (and it is a special case of the extended phenotype)." (Dawkins 2004)

some, but not all, of the consequences of niche construction." (OLF 2003:131[1]). In a number of papers, they give and repeat several reasons. We will examine their arguments below, but for the most part, we will not agree. Rather, we will show a subtle manner to reconcile both OLF and Dawkins.

3.9 Niche construction and extended phenotype

OLF (or rather, Laland *et al.*, see the following references) see several reasons not to consider niche construction as an avatar of phenotypic extension: (1) "the relationship between genes and niche construction" (Laland & Sterelny 2006:1756, repeated in Laland *et al.* 2007:54, Laland *et al.* 2009:199, see also Odling-Smee 1988:85) (2) the "reciprocal causation" between construction and selection (OLF 2003:19, repeated in Day *et al.* 2003:83, Laland & Sterelny 2006:1757, Laland *et al.* 2007:54, Laland *et al.* 2009:199) (3) the evolutionary importance of feedbacks and in particular feedbacks stemming from "mere effects" (Laland *et al.* 2005:53, repeated in Laland *et al.* 2007:55) (4) their "desire to focus on the symmetry between organism and environment" (Laland *et al.* 2005:53) (5) their desire to "bring a fresh perspective" and "develop [it] into a viable empirical programme of research" (Laland *et al.* 2005:53). Here, for presentation convenience we will discuss only (1) and (2) ; (3) will be discussed just in the following section (3.10), we already discussed (4), (5) will be examined later (sections 3.13 and 5).

The relationship between genes and niche construction

Laland and Sterelny (2006:1756) state their argument as follows: "First, it is just not true that all evolutionarily consequential niche construction is under genetic control. This is well illustrated by the example of the coevolution of dairy farming and lactose absorption. (...) There are no ''genes for'' dairy farming (*sensu* Dawkins 1976), and it is not an adaptation (*sensu* Williams 1966). The difference between the cultures that farm cattle and those that do not are not explained by genetic differences between the two types of populations. In this example, niche construction is not reducible to the prior natural selection of genes controlling niche-constructing behavior, yet this activity has generated stable selection favoring genes for lactose absorption. (...) Thus, human cultural niche construction must be recognized as a significant cause of human evolution."
Then, they give many other examples of such cultural niche constructions that are in their view not reducible to prior natural selection. If niche construction can be non-genetic in origin, then our framing of niche construction in genetic terms is in trouble. But is this really the case?
Let's dwell on this example. It is a famous example of niche construction (see also *e.g.* OLF 2003:343, Laland 2004:322-323, Laland & Brown 2006:97, Laland *et al.* 2007:55, Laland *et al*. 2008:551, Laland *et al.* 2009:198), but it is perfectly reducible to classical natural selection.
We are facing different human groups that are supposed to be genetically homogeneous with respect to dairy farming, but culturally heterogeneous (again with respect to dairy farming).

1 The original quote is the other way around : "One theoretical construct that captures some, but not all, of the consequences of niche construction is Dawkins' (1982) extended phenotype."

There are two ways of accommodating cultural heterogeneity in a gene-centrist view: either you include parental cultural practices into the dimensions of the offspring developmental environment, and you treat cultural heterogeneity as a reaction norm ; or you just treat culture as a developmental noise at the level of the group (groups randomly "fall", or even do not fall, into different cultural gaps). The first line of reasoning supposes that there are "genes for" culture (*sensu* Dawkins 1976-2006:37), and that their corresponding adaptation, if any, is "the capacity to learn" (OLF 2003:21, Laland & Sterelny 2006:1756, see also Sterelny 2005:13). The second line of reasoning supposes that there are no such genes and that to espouse or not culture is, from a genetic point of view, a matter of chance. In any case, what we observe here is not niche construction[1], but either classical (one way, here) coevolution between "genes for" culture and "genes for" digestion (section 3.7), or classical natural selection of "genes for" digestion driven by external events (here cultural ones).

Culture might seem too central and too vast to us to be treated as a reaction norm or as a developmental noise. We might want to think it as a very process in evolution, as for instance in cultural evolutionary studies. This possibility exists, but it is a matter of explanatory emphasis[2], not of breaking any explanatory asymmetry between natural selection and niche construction in the selectionist scheme, as we just showed above (we temperate this claim in section 4.2).

The "reciprocal causation" between construction and selection

Here is one arguments of OLF against an explanatory hierarchy between natural selection and niche construction (explanatory hierarchy *sensu*: selection would explain construction but not the other way around), for which our framework of time-scale separations will show relevant:

"Yet the standard view is that niche construction should not be regarded as a process in evolution because it is determined by prior natural selection. The unstated assumption is that the environmental source of the prior natural selection is independent of the organism (...). However, in reality, the argument that niche construction can be disregarded because it is partly a product of natural selection makes no more sense than the proposition that natural selection can be disregarded because it is partly a product of niche construction. One cannot assume that the ultimate cause of niche construction is the environments that selected for niche-constructing traits, if prior niche construction had partly caused the state of the selective environment (...). Ultimately, such recursions would regress back to the beginning of life, and as niche construction is one of the defining features of life (...) there is no stage at which we could say natural selection preceded niche construction (...)." (OLF 2003:18-19,375, repeated in Day *et al.* 2003:83, Laland 2004:319, Laland *et al.* 2009:200; close arguments are found in Odling-Smee 2007:282 and Laland *et al.* 2008:552)[3].

1 *Sensu* auto-niche construction, for allo-niche construction is, as we explained earlier, classical natural selection.

2 Explanatory emphasis : we mean here that in this example, the theoretician can focus on cases where the "genes for" culture are at an evolutionary steady state while "genes for" digestion and "culture for" dairy farming are evolving. Thus the theoretician would probably like not to invoke any selection on "genes for" culture.

3 Elsewhere, the authors adopt a more temperate view : "[W]e are proposing a mix of externalist and constructivist explanations, according to which natural selection is partly dependent on the niche-

Though intuitive, this argument does not support close examination. For the question is not whether we *can* trace some factual "dialog" between selection and construction back to the origin of life, but whether we *need* to trace this dialog in our explanations. In other terms, the question is whether, at a time (in the history of life), some invariants enabling to apply an externalist selectionist scheme at some interesting time-scale emerged. In our case, the first long lasting, faithfully, differentially, replicating entities set the stage for selection. (They did not, however, rule out the possibility of construction, as we will see in section 3.10.)
Of course niche construction can (have) set some initial conditions. So did the origin of the solar system, the big bang (if any), and so on. But initial conditions do not have the same status than processes in dynamical systems.

Conclusion on extended phenotypes

Extended phenotypes, *sensu* phenotypes extended in space, belong gloriously to the cohort of cases that an externalist, gene-centrist, selectionism aims at explaining. The same would hold for extended phenotypes of organisms (Turner 2000) in an organism-centered view if the organisms are faithful enough units of replication. Certainly do the phenotypes extend beyond the organism's boundaries, but Dawkins (1982) shows that it does not matter much for the selectionist scheme. Rather, he shows that genes' phenotypes are always somewhat extended, and that the fact that the phenotypes are extended does not prevent us to identify independent selection pressures (this fact is acknowledged by OLF 2003:131). If phenotypes extended in space pertain to the most orthodox externalism, as they seem to be, there is no reason to make them a case of niche construction, nor to reduce niche construction to extended phenotype.
Thus, if niche construction is founded, this part of the Dawkinsian scheme should not capture any of the consequences of niche construction (here we do agree with OLF 2003:131). Actually, the spatial extension of the constructed environments is not what primarily matters (see sections 3.10, and 2.5).

3.10 Niche construction and posthumous phenotypes[1]

Apart from the spatial extension of environmental modifications, another idea pervades niche construction theory : the idea of evolutionary feedback. As we shall see, spatial extension of phenotypes should not be seen as anything else than a mean to cause evolutionary feedback on our time-scales of interest. We will claim here that feedback, not spatial extension, is what truly distinguishes niche construction theory from the selectionist scheme.

Niche construction and feedback

In their concluding chapter, OLF put their view in a nutshell. It is worth quoting at length : "… Consider the differences it makes if natural selection stems from autonomous components

constructing activities of organisms, and niche construction is largely dependent on prior natural selection pressures, including those that are, or have been, biotically modified." (OLF 2003:373). The spirit remains the same : the claim that niche construction is not the mere product of natural selection, but an evolutionary process in itself (*e.g.* OLF 2003:370).

1 Among all other parts of the text, the section 3.10 has benefited from invaluable discussions with Maël Montévil.

of environments or from niche-constructed components of environments. The difference can be summed up in one word : feedback. If organisms evolve in response to selection pressures modified by their ancestors, there is feedback in the system. (…) It is well established that systems with feedback behave quite differently from systems without feedback (Robertson 1991), and by neglecting this feedback, the standard evolutionary perspective must at least sometimes misrepresent how evolution works. (…) For example, [models show that] feedback from niche construction can cause evolutionary inertia or momentum, lead to the fixation of otherwise deleterious alleles, support stable polymorphisms where none are expected, eliminate what would otherwise be stable polymorphisms, and influence linkage disequilibrium." (OLF 2003:376. This corresponds to argument (3) listed in section 3.9. This argument is also found *e.g.* in Laland *et al.* 1999:10242, Day *et al.* 2003:88, Laland 2004:320, Laland *et al.* 2005:53, Laland & Sterelny 2006:1754, Laland & Brown 2006:96, Laland *et al.* 2007:56, Laland *et al.* 2008:202. For an extensive, gene centered, adaptive dynamics modelling of phenotypes extended in space and time, see Lehmann 2007.)

Above (section 3.8), we made the assumption that niche construction could not stem from a modification of the phenotype-fitness map (the selective invariant) by the phenotypes, because such a dependence of the selector on the selected would hardly allow to make sense of any "selection". Thus, we consider that the selective invariant is "autonomous"[1]. There is another way to make sense of niche construction, however.

Niche construction rephrased

Niche construction, being an effect of a gene on its environment, is a phenotype. As a phenotype, the dynamics of the construction can be thought of as an ontogenesis[2]. If the

1 As OLF use the term "selective environment", which is let undefined in their book (though they cite Brandon & Antonovics 1996, but for another purpose, OLF 2003:30), the two views are not necessarily contradictory (see sections 3.13, 4.2 and glossary).

2 To our knowledge, the fact that standard theory ignores development and that niche construction precisely "arises from development" (OLF 2003:381), has been only lately pointed out by Laland *et al.* (2008:549). For instance, we have not been able to find any mention of the term "EvoDevo" in their book, though the two views appear very similar. There is a notable exception however, to be found in the summary of the 4th chapter :

"It is only because ontogenetic processes can be semantically informed by natural selection that individual organisms can survive and reproduce and contribute to the next generation of their populations. Thus, niche construction fuels the evolutionary process as a consequence of the interactions of individual organisms with their environments, while natural selection informs the evolutionary process by selecting for "fit" genotypes. The result is an intimate interplay between phylogenetic and ontogenetic processes in evolution. Neither process on its own suffices to account for either the evolution of populations or the development of individuals. Together hey help to account for both." (OLF 2003:193, the paragraph is repeated p.381)

Here, "intimate interplay" really looks like "entangled time-scales" (in our terminology).

By contrast, most of the time we find arguments like this one :

"The effects of genes on a phenotype, whether the phenotype is the carrier of the genes or another individual, are mediated by developmental (including environmental) processes, and to leapfrog those processes is tantamount to denying that development exerts any meaningful influence on the phenotype." (OLF 2003:372).

Note that this is not what classical selectionism denies : it denies that developmental dynamics exerts any meaningful influence on evolution (or rather selection). In another instance we find the argument properly dynamics of the constructed environment has to be taken into account in a selection process, this means that the ontogenesis dynamics is not separable from the selection dynamics. In other terms, ontogenesis lasts "too long" to be separated from selection.

Now we can rephrase niche construction theory into a single sentence : *ontogenesis is not separable from selection*[1]. From the analytical perspective we adopted, this is the central claim of OLF ; beside, it stems directly from Lewontin's works (1983). We were not able, however, to find it obviously stated[2]. We are going to examine this claim in details.

How is it possible that ontogenesis lasts too long comparatively to the focal selective process ? There are two (compatible) possibilities :

(1) our time-window of interest is too small : for instance, we are studying selection at an intra-generational scale, where ontogenesis dynamics is primary (this case is rather obvious and we will not study it here, though, as we evoked above, most empirical works deal with such time-scales, see Endler 1986)

(2) the phenotypes extend in time on several generations : this is particularly the case with "posthumous phenotypes" (Lehman 2007). In some cases though, it will be possible to apply the classical selectionist scheme (*sensu* the selectionist scheme separating ontogenesis from selection) on niche constructing activities with a suitable change in the variables (and sometimes a rescaling of our time window of interest) : we will not consider selection on genes, but on lineages. Lineages are genealogical chains of genes, they extend on several generations of genes ; how many is precisely the question to answer.

First, we will give several examples of niche construction extending in time, then we will discuss the notion of posthumous phenotype and its relationship to evolutionary feedback.

Examples of posthumous phenotypes

The simplest cases of phenotypes extending in time are probably maternal effects. As stated by OLF (citing Mousseau and Fox 1998, see also Wolf & Wade 2009), "maternal effects occur when a mother's phenotype influences her offspring's phenotype independently of the female's genetic contributions to her offspring." (2003:125, see also the discussions pp.9-11,

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stated :

"For instance, Dawkins' approach neglects niche construction resulting from by-products and other non-adaptations, which can equally be consequential. Also, once we recognize that there is a second route by which phenotypes play a role in evolution, and a second form of feedback from niche-constructing effects, it opens the door for a multitude of developmental processes, acquired characters, social learning and culture to be instrumental in the evolutionary process, through their influence on niche construction. For example, it grants phenotypes a limited capacity to co-direct the genetic evolution of their populations by recruiting ontogenetic processes to modify natural selection." (Laland *et al.* 2005:53)

1 Niche construction theory, strictly speaking, is a particular case of non-separability, where the non-separability stems from the non-separable effects of ontogenesis on the selective dynamic. Indeed, theoretically, selection can be non-separable from ontogenesis because of a selective environment varying "autonomously" at the same pace than ontogenesis. "Selective environment", however, is a fuzzy concept. We could as well consider that any (non neutral) phenotype is a modification of the selective environment (see right below) and thus, that whenever ontogenesis is not separable from selection, the selective environment cannot be said to be totally autonomous (see also section 4.2).

2 For instance, see this statement of Laland *et al.* (2005:39) : "[The fact that] instances of niche construction that are neither deliberate nor obviously beneficial to the constructor can nevertheless direct its subsequent evolution (...) is our major focus "

125-127, 161 ; for a taste of the dynamical effects at the population dynamics scale see Ginzburg & Collyvan 2004:49-63). Thus, the parental phenotype lasts in the descent. This implies that, if we are seeking any evolutionary explanation of maternal effects, the right time-interval of phenotypic expression to consider is not one generation, but (at least) a couple of generations. The wrong way to tackle the issue would be to consider the costs (or benefits) of a mother's strategy without considering also the impacts on offspring. Thus, the "unit of selection" here, lasts (at least) two generations.

An example of a phenotype "more posthumous" than a maternal effect can be found in the beaver dam. Beaver dams can last for decades or even centuries (Ruedemann & Schoonmaker 1938, Neff 1957, Meentemeyer & Butler 1995, cited in Martell *et al.* 2006), with a generation length of approximately five years (Millar and Zammuto 1983). Though, a selectionist account of dam building can be provided : "For Dawkins (…) when beavers build dams they ensure the propagation of 'genes for' dam building, and that is all. Linear causation is maintained." (Laland 2003:317[1]). Indeed, beavers directly benefit from their dam. But probably, dams can be inherited (Laland *et al.* 2003:119), and beavers can benefit from their ancestors' dams, which leads to kin selection in time. Here too, if we were to explain any tendency for beavers to produce long lasting dams, the evolutionary explanation could gain from being stated in terms of multigenerational units of selection.

The effects of earthworms on land can last even more than beavers' (in numbers of generations). As Laland *et al.* (2005:39) put it, "… each worm directly benefits from its own [burrowing] activities" but "their impact on the soil accumulates over many generations". In particular, earthworms "weaken soil matric potentials, allowing the organism to draw water into its body, thereby preventing desiccation (Turner 2000)." This might explain why earthworms seem so poorly adapted to life on dry land (Turner 2000). This is one of OLF's favourite examples (see also *e.g.* OLF 2003:11,160,291,375, Laland 2004:319-321, Laland & Brown 2006:99, Laland & Sterelny 2006:1754,1758-1760, Laland *et al.* 2008:552,554,560, Laland *et al* 2009:199). Here, we can notice that the covariation between a parental impact on the environment (say, the soil matric potentials) and the effect on offspring's fitness seems weaker than with the beaver dam, where the covariation seemed weaker than with maternal effects.

Then, we have another paradigmatic case : the production of oxygen. "When photosynthesis first evolved in bacteria (…) a novel form of oxygen production was created. The contribution of these ancestral organisms to the earth's 21% oxygen atmosphere must have occurred over billions of years, and it must have take innumerable generations of photosynthesizing organisms to achieve. It is highly likely that modified natural selection pressures, stemming from the earth's changed atmosphere, played an enormous role in subsequent biological evolution." (OLF 2003:12). Here, we have an environmental impact that is so small at the *per capita* level, that it will take (thousands of) billions of generations to be evolutionarily significant. The "feedback" is so slow that there seems to be no feedback.

1 We are quoting out of context here because Laland regrets that Dawkins does not consider impacts of dam building genes on other loci, which is, in his view, a new scope for niche construction. However, Dawkins (1982) gives many examples of intra- and inter-genomic coevolution, thus we are not sure to get Laland's contention.

Posthumous phenotypes and scale separability

Now we can specify the notion of posthumous phenotype. This is necessary if we want to understand the difference between saying that genes have posthumous phenotypes, and saying that genes modify the "selection pressures" (a difference not highlighted in Laland's quote above, section 3.8). A phenotype is a modification in the environment that can be attributed to a gene. At first sight, there is nothing wrong with the idea that this environmental modification can last longer than its constructing gene (*sensu* nucleic acid), as there seems to be nothing wrong with the idea that a phenotype can extend beyond gene's boundaries. Thus, posthumous phenotypes are to time what extended phenotypes are to space. There is a difference, however : time is the reference dimension for dynamical systems.

Classical phenotypes (or rather phenotypes in classical studies) are environmental modifications whose dynamics are thought to be separable from the selective process' dynamics : they are brief enough to be considered as instantaneous. Posthumous phenotypes, however, persist in time, and as persistent entities, they can impact the selective dynamics: it is, at first sight, no longer separable from ontogenesis. Is it still possible to apply the "classical" selectionist scheme separating ontogenesis from selection ? There are four possibilities here :

(1) the posthumous phenotype has fast enough a dynamics (short lifetime) compared to the selective process' dynamics it undergoes (*i.e.* weak selection[1])

(2) the posthumous phenotype has a dynamics comparable to that of the selective process

(3) the posthumous phenotype has slow enough a dynamics compared to the selective process' dynamics (*i.e.* "weak phenotype")

(4) the posthumous phenotype has no characteristic time-scale.

Moreover, these comparisons are made on our time-scale of interest (except for 4). Here for simplicity, we do not consider the characteristic time-scale of genes (modified by mutation[2]), but it should be included into a complete analysis (we discuss it briefly in section 5.2). The characteristic time-scale of the selective process depends on fitness differences (with neutral phenotypes, *i.e.* "mere effects", the selective time-scale is infinite). The fact that the current fitness differences might depend on the selective process itself (*e.g.* in frequency-dependence) leads to the interesting possibility that a focal case can jump from one class (1, 2 or 3) to another during the selective process. This is, of course, also true with classical one-generational phenotypes.

In cases (1) and (3), the two dynamics are separable and the classical selectionist scheme applies. In case (2) and (4), we have what we could call, now, true niche construction. Let's take a look at our examples one more time.

Scale (non) separability by example

Maternal effects and beaver dams would belong to case (1) (let's assume it for the sake of argument, even if we do not *a priori* know the dynamics of the selective process involved).

1 On weak selection, see Wu *et al.* 2010.

2 For a n bases gene, with a probability of μ mutations per generation per base, the characteristic time-scale is approximately $1/(n\mu)$ generations (of course, the characteristic time depends on our criterion for genetic identity).

They involve kin selection in time, as extended phenotypes can involve kin selection in space. The probability that a “gene for” a posthumous phenotype invades depends on its posthumous effects on its descent's fitness, this amounts to tracking the kin selection pressure at several generations in the descent (Lehman 2007:6,10). This approach is particularly suited under weak selection and additive gene action (Lehman 2007:14). This is the first way to understand the evolution of posthumous phenotypes within the classical selectionist scheme. Another way is to consider selection on rescaled (*i.e.* multigenerational) lineages having rescaled phenotypes. The rationale for rescaling is that probably, the one generation time-interval or the one individual space-interval are not the most suited to understand every biological cases. We give it here as a theoretical possibility, without entering into mathematical details that would depend on focal cases. For posthumous phenotypes, we rescale in time ; for extended phenotypes, in space (for space, see Van Baalen & Rand 1998). The less we have to rescale to get a consistent picture of what is going on in the selective process, the smaller our unit of selection (in space or time)[1]. When rescaling (in space or time, but it is time that matters here), we define our genotype-phenotype and phenotype-fitness maps on broader intervals than the usual ones (actually, for the first map, we would rather speak in terms of lineage-phenotype map). The lineage has to be defined with respect to a number of generations (a genotype is a one generation lineage) : it is the set of the gene copies on the given time interval. The lineage has an ontogenesis across generations, as a genotype has an ontogenesis across a single generation (sometimes we could consider even smaller time-intervals) : the lineage's phenotype is the set of gene copies' phenotypes on the given time-interval, including possible interactions in time. As long as the rescaled hereditary entities and their corresponding phenotypes have dynamics that are separable from that of the rescaled selective process, the classical selectionist scheme separating ontogenesis from selection applies. Rescaling is particularly suited for cases where genes have non additive posthumous effects and when lineages have somewhat identifiable beginning and end, though time boundaries are not, in our view, necessary[2]. We propose a slightly formalized account to clarify this point below.

Photosynthesis would belong (quite undoubtedly this time) to case (3). As we mentioned above, atmospheric enrichment in oxygen is “too slow” and seems at first sight negligible as well. Let's note, however, that “slow” here depends on our time-scale of interest : if we are dealing with selection extending on thousands of billions of generations, then the selective process can indeed be affected by construction on our time-scale of interest. Unless we are

1 This does not mean that the phenotypes do not extend beyond the spatial or time unit. The spatial or time units of selection are special cases of classical units of selection (Lewontin 1970), which can be obtained in mean field situations (defining groups of entities does not imply any spatial arrangement of these entities).

2 With unbounded in time lineages, the spirit of rescaling is to take enough generations in the cutting to be able to neglect the remaining posthumous phenotype of the lineage. Neglecting the remaining posthumous phenotype is what we do when we neglect maternal effects at one-generational scale (though maternal effects are, except spontaneous generation, ubiquitous). An example of such quasi-unbounded in time but evolving lineage can be found in the quaking aspen (*Populus tremuloides*) (Bouchard 2008). In this case, assuming weak selection, we can derive Hamilton's rule (see below) either for invasion of the tree by some of its parts or for invasion of an area by a tree (tree here means the whole “forest” of ramets).

dealing with billions of generations however, we cannot think of lineages of photosynthetic organisms being selected for enriching the atmosphere : on time-scales smaller than billions of generations there is no selective feedback on atmosphere enrichment, and atmosphere enrichment is “a mere effect”. This does not mean, of course, that there will necessarily be a selective feedback on longer time-scales : O^2-rich atmospheres can be neutral with regard to photosynthetic organisms (or “genes for” photosynthesis).

In between, let's say we have earthworms, exemplifying case (2) (once again, let's assume it for the sake of argument, even if we do not really know the involved time-scales). The case is more difficult. We cannot rescale our system to separate a selective process and an ontogenetic process, even a multigenerational one, as the two processes have the same time-scale. If we try some rescaling, either we will assess phenotypic values and fitnesses on the relevant ontogenetic time-scale (that is close to that of the selective process), and selection will not have enough time to occur ; or we will assess phenotypic and fitness values on small enough time-scales for selection to occur, but we will ignore some evolutionarily relevant parts of the ontogenetic process. Facing this difficulty, the first solution is to modify our time-window of interest : to shorten or expand it. Shortening the window enables, hopefully, to neglect some long term aspects of the phenotypes. This is what we do intuitively when we consider the evolution of photosynthesis: we do not consider, at first sight, the possible feedback of O^2 enrichment occurring on a billions of generations time-scale ; we focus on shorter time-windows. Widening the window enables, hopefully, to identify a longer selective process and to perform a rescaling as described above. This is what we would intuitively do if, for instance, we were studying selection on photosynthesis on cosmic time-scales (which is an approach that deserves respect), where O^2 enrichment can be an evolutionarily relevant aspect of the photosynthetic lineage(s)'s phenotype. Instead of rescaling the window of interest, the second solution is to give up the primacy of selection in our explanations, and to study the interplay between ontogenesis and selection. This is what we should intuitively do when considering selection at an intragenerational time-scale, where the trends in the phenotypic distribution cannot, hopelessly, be given by selection alone. The “interplay” between ontogenesis and selection here does not mean that the phenotype-fitness map varies throughout ontogenesis, but that the phenotype varies throughout the selective process (in other terms, the genotype-phenotype map is a dynamic map, not an instantaneous one, compared to the selective process). To conclude, the selectionist scheme *does* apply (if the conditions of inheritance and differences in fitness are met), but it is insufficient (*sensu* dynamical insufficiency, Lewontin 1974).

In case (4), the phenotype has no characteristic time-scale. This means that it continues to have significant effects (variations or fluctuations), that is, it continues to “last”, on all time-scales. This is given here as a theoretical possibility (we cannot give any biological example of such a case, which does not mean that there is none). It has to be treated as case (2), except that we cannot enjoy the possibility to rescale our time-window of interest, because the phenotype will have significant effects on the same time-scale than any rescaled selective process. We cannot identify any unit of selection in time even on infinite time-scales. The selectionist scheme will apply (if the conditions are met) but will always be insufficient. (Let's quickly note that, even if we do not consider this issue here, the same reasoning would hold for extended phenotypes having no characteristic space-scale. In this case, we would not be able to identify any spatial unit of selection and the phenotype-fitness map would not be defined, in the sense that the phenotype's fitness would show relevant variations at all spatial scales[1].)

Rescaling: some formalism

To specify our point, we can give the following metaphorical formalism. The question is: what is the condition of invasion, on a given time-interval, of a gene having posthumous phenotypes in a population of genes bequeathing no legacy? Assuming that fitness is a multiplicative property, we have the following condition:

$$\prod_{t=0}^{\tau} w_p(t) > \prod_{t=0}^{\tau} w$$

where w stands for the absolute fitness of the resident gene and is assumed to be constant, w_p(t) stands for the absolute fitness of the gene having posthumous phenotypes, and τ is the characteristic time of the posthumous phenotype. w_p(t) is a function of the net change C of constructing the posthumous phenotypes (here C is assumed to be constant) and of the change $B(t', t\text{-}\tau \leq t' \leq t)$ stemming from the dynamics of the posthumous phenotypes bequeathed by past generations. B is an integral in the case of additive processes (chemical production for example), possibly convoluted with a decay function. (Here for simplicity, we assume that the posthumous phenotypes only affect clonal descendants, *i.e.* the relatedness coefficient R = 1. In the third chapter of this thesis, we will model explicitly the opposite case.) We can write the following expression for w_p(t):

$$w_p(t) = w + B(t', t-\tau \leq t' \leq t) - C$$

A time t, the invasion condition is:

$$B(t', t-\tau \leq t' \leq t) - C > 0$$

Assuming additive gene action on fitness, we get:

$$B(t', t-\tau \leq t' \leq t) = \sum_{t-\tau}^{t} B(t)$$

where $B(t)$ is the change in fitness at the present time arising from a phenotype constructed at time t. In this case, our invasion condition can be rewritten:

$$\sum_{t-\tau}^{t} B(t) - C > 0$$

which is Hamilton's rule for kin selection in time (Lehmann 2009). Assuming weak selection, we consider that $B(t', t\text{-}\tau \leq t' \leq t)$ is at a steady state, and the fulfilment of the condition is a robust predictor of invasion (stochasticity let aside)[2]. However, if gene action is non-additive, we have to stay with $B(t', t\text{-}\tau \leq t' \leq t)$ and possibly no steady state is never attained. In this case however, a tractable case occurs when we are able to identify a pseudo-life cycle at the unit of the lineage. We can write:

1 In the special case (point with null probability) where the selective process is strictly "parallel" to the phenotype, the integral of fitness on space is either zero, or minus infinity or plus infinity. We do not go into details here, as this is given foremost as a limit case.

2 Moreover, it should be noticed that weak selection somehow entails additive gene action, in the sense that small perturbations of fitness can be thought to be additive.

$$W_p = \prod_{t=0}^{\tau} w_p(t)$$

where W_p stands for the rescaled fitness of the lineage, and $w_p(t)$ for the fitness of its units. $w_p(t)$ is still untractable but now we can identify a rescaled selective process:

$$W_p = S(G_p, E)$$

where G_p is the focal piece of lineage and E the relevant environment for the lineage.

Conclusion on posthumous phenotypes

OLF's argument against an explanatory hierarchy between natural selection and niche construction (the "reciprocal causation" issue examined above, section 3.10) requires that living systems are in case (4), or in case (2) with a phenotype's characteristic time comparable either to the duration from the origin of life or to the gene's characteristic time (these two conditions ensure that we cannot resize our time-window to identify an autonomous selective process). The central figure of niche construction theory (OLF 2003:14:fig.1.3, reproduced as fig.1 below) has to be understood in the same way.

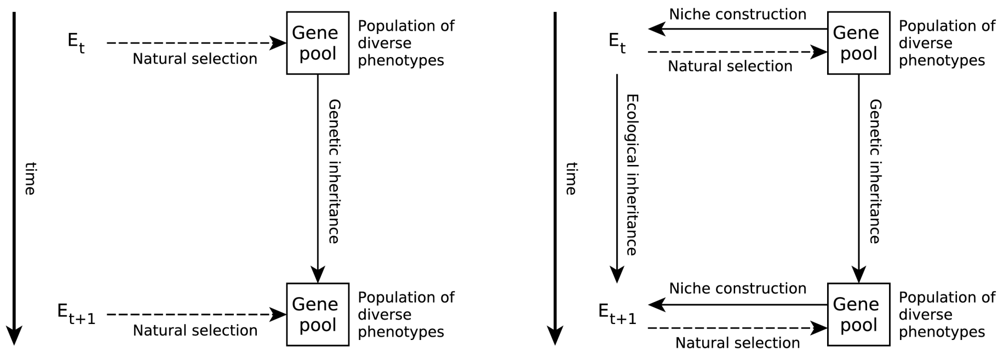

Fig.1: The tragedy of arrows. It is a truism that like other models, pictures are misleading when crucial hypotheses are, consciously or not, not made explicit. OLF give the following caption for their figure : « [Left] : Standard evolutionary perspective : Organisms transmit genes from generation t to generation t +1 with natural selection acting on phenotypes. [Right] : With niche construction : Organisms also modify their local environment (E), as depicted by the arrow labeled "niche construction." Each generation inherits from ancestral organisms both genes and a legacy of modified selection pressures, described as "ecological inehritance.". » As the reader will guess, niche construction theory (right) is founded only if the processes described by parallel arrows have the same time-scale (and interact). To give empirical evidences for such additional arrows is insufficient to support the theory if the time-scales and characteristic times are not specified. (After OLF 2003:14:fig.1.3)

To conclude, as for posthumous phenotypes, we evoked two ideas. The first is the question of separating the ontogenesis of a phenotype, possibly a rescaled one, from the selective process it undergoes. The second is the question of the size of our time-window of interest, that is directly linked to the scales of the observable processes, and that should be mentioned in

debates (implicitly) relating to the non-separability of some processes.
How much of evolutionary biology conforms to dynamics such as (1), (2), (3), or (4) is an empirical issue. Not an easy one, of course. To our knowledge, none of the empirical examples given by OLF (mostly in 2003:chap.2) has been shown to conform to case (2) or (4) where ontogenesis is not negligible. If we are right in rephrasing niche construction theory as the non-separability of ontogenesis and selection, this means that there is, to date, no known example of true niche construction (or at least that they are not given by OLF). Only better : niche construction may be the hidden face of the darwinian moon.

3.11 Relaxing the invariance of the phenotype-fitness map

Theoretically, we can relax the assumption that the phenotype-fitness map is invariant with respect to time on our time-scale of interest. This is in particular the case if we make it depend on catastrophic events. This means that condition (2) in the selectionist scheme (section 2.1) is not met : even given all relevant environmental conditions, a phenotype does not have any fitness. In this case, fitness as an evolutionary currency is ill-defined[1]. A comparison can be made with economy, where price can also be undefined, in which case there is no trade or crisis (*e.g.* Green & Zhou 2004:8, Walter & Brian 2007, Mandelbrot & Hudson 2009). We would not get any robust insight of what is "selected" for "the good of" what. Natural selection, and the selectionist scheme as an explanatory scheme, would vanish. Other theories, neutral theory for instance, would take over (of course such other theories can also be relevant when fitness is defined).
If constructionists want to integrate natural selection to an extended theory (including niche construction), they should be clear that the phenotype-fitness map, *i.e.* the selective invariant, is not modified by niche construction.
There could be another way to consider the relationship between natural selection and niche construction, however. Constructionists could consider that natural selection, *sensu* invariance of the phenotype-fitness map, is a limit case of "extended evolution" including niche construction as a more general invariant, as Newtonian mechanics can be considered as a limit case of relativity (Rivadula 2004, see Lewontin 1983:275 for a similar comparison). We do not explore this issue here, but in both ways, the invariants of the extended evolutionary theory should be specified.

3.12 A note on evolutionary self and non-self

Niche construction is framed in terms of self and non-self (see also our discussion of auto- and allo-niche construction in section 3.4) : niche construction is "the process whereby organisms (…) modify their own and/or each other's niches. Niche construction may result in changes in one or more natural selection pressures in the external environment of populations. (...)" (OLF 2003:419). Debaters should be careful in agreeing on what "own" or "other" mean (here we will discuss only "own", or rather self, letting to reader's discretion the completion by the reciprocal). Depending on the time-scale of the modification of the niche, there are two meanings of "self" in niche construction claims:

1 As evoked above, a similar problem arises if we consider the theoretical possibility of extended phenotypes having no characteristic spatial scale.

(1) “self” refers to the individual bounded by classical generations (a given organism, if identified, or a given piece of germinal nucleic acids)
(2) “self” means one's descent (i.e. the individual is a lineage).

If “self” refers to the individual, modifying its own niche can be thought of as a classical, possibly extended, phenotype. If “self” refers to one's descent, then the account given in section 3.10 holds. It should be noticed that rescaling, when possible, consists precisely in shifting from one meaning of “self” to another. This point is important, to appreciate how synonymous it can be to say that an organism (or a gene) bequeaths modified “selection pressures” to its descent (that is, to itself later in time), and to say that a lineage has a phenotype[1]. Whenever we rescale (even implicitly), we have synonymy.

Note : here we did not come back on the oscillation between individuals and populations contained in the definition, but it may be worth being looked after too (see sections 2.3 and 3.4).

3.13 Concluding discussion on what niche construction is

Niche construction revisited : definitions and invariants

Niche construction is defined as “the process whereby organisms (…) modify their own and/or each other's (…) selection pressures » (OLF 2003:419). We have seen that this definition is problematic, though not meaningless, in several respects : (1) the meaning of “organism” (2) the meaning of “selection pressure” (3) the meaning of “self” (4) and the (unspecified) time-scales of interest.

As for (1), we have argued that we should rephrase niche construction in genetic terms. This makes most cases of organisms modifying their “selective environments” reducing to cases of genes having extended phenotypes (extended s*ensu* beyond organism's boundaries). As for (2), we have stressed the necessity to clarify whether one understands selective pressures as a selective invariant (the phenotype-fitness map) or a variable (the selection coefficients) of the selective process (see also section 4.2). If we consider selection pressures as variable selection coefficient, niche construction theory is somehow trivialized as a particular case (possibly of tantamount importance, but already described by standard theory) of natural selection. If we consider them as the long term selective invariant, we argued that we still should not consider that they are modified, but that, instead, the phenotype is dynamic. As for (3), we have stressed the necessity to be clear about the level (in time) of construction (*e.g.* individual or lineage). As for (4), we have examined at length the embedded implications of choosing a time-scale of interest and to slip from one to another (*i.e.* to possibly implicitly, unconsciously, rescale the problem when debating).

We rephrased evolutionary niche construction theory into a single sentence : “ontogenesis is

1 Recall Laland's quote (2004:320): “... some extended phenotypes are ‘heritable’. Organisms not only acquire genes from their ancestors but also an ecological inheritance, that is, a legacy of natural selection pressures that have been modified by the niche construction of their genetic or ecological ancestors (Odling-Smee 1988)”.

The same reasoning holds when we want to compare the claim (encountered sometimes) that organisms or genes bequeath modified “selection pressures” to themselves (as individuals) later in time, and the claim that they have phenotypes on their whole lifetime.

not separable from selection". Ontogenesis is the process whereby a gene modifies its environment ; thus, phenotypes are always extended. Ontogenesis is defined by the genotype-phenotype map. Selection is the process whereby a phenotype awards fitness to the gene (or the lineage) that produces it. It is defined by the phenotype-fitness map. In our view, the two maps are invariants even in niche construction theory, but when ontogenesis is not separable from selection the genotype-phenotype map is dynamic, and this dynamics has to be taken into account. If we conflate the two maps however, the point that natural selection is not modified is obscured.

We proposed that for some cases, non negligible posthumous modifications of the environment could be accounted for within a classical selectionist way with a proper rescaling in time of the considered lineages, phenotypes, and selective processes. Under weak (*i.e.* slow) selection and additive gene action, rescaling is unnecessary, and we can apply a kin selection in time approach (Lehman 2007, 2009). However, we have emphasized that rescaling is not, from a theoretical point of view, always possible. Thus truly new dynamics are possible.

We have seen that all (but one : the notable argument on feedback) arguments of OLF in favour of niche construction theory do not hold, and that none of their empirical examples truly exemplify it, in the sense that *a priori,* they can be as well explained by the classical selectionist scheme (by the way, these examples are given as absolute numbers, not relative numbers, which would weaken the claim on pervasiveness of niche construction if these examples exemplified it[1]). Throughout the presentation, we have put a special emphasis on the fact that claims about the time-scales of processes are empirical claims, and that to our knowledge no data, for the moment, justifies an entanglement of ontogenesis and selection. We should limit our invocation of niche construction to those cases where construction is *probable*, not just *possible*.

Notably, OLF (2003:Chap.7) propose empirical methods for detecting evolutionary niche construction in the wild. We did not review this program here, but in our view, it reduces unfortunately to seeking for evidences of evolution of extended phenotypes or intra-genomic coevolution, notably the following method: "Step 1 : Search for a correlation between some organismal structure and environmental factors. Step 2 : If no relationship is found, investigate whether the organism exhibits niche construction that might compensate for poor adaptation of the structural trait. Step 3 : Investigate whether there is evidence for organism-driven modification of the selective environment. Step 4 : If so, search for evidence for evolutionary feedback in the form of structural or functional adaptation to the constructed environment." (OLF 2003:292). In our view the method can be rephrased as follows : "Step 1 : unchanged, Step 2 : search for adaptation in the form of extended phenotypes. Step 3 : unchanged. Step 4 : search for intra-genomic coevolution."

However, niche construction theory, properly rephrased, is a theoretically valid extension of standard evolutionary theory (where ontogenesis is separated from selection), and we feel that it is worth investigating. This entails that the invariants of the extended evolutionary theory should be explicit (we proposed general invariants above), and that the empirical facts should be gathered with respect to these posited invariants.

1 *E.g.*, in addition to OLF 2003:chap.2, Laland & Sterelny 2006:1756, Laland *et al.* 2007:57, Laland *et* al. 2008:551, Laland *et al.* 2009:203.

Other constructionist tracks

Here, we have dealt with only one time-scale separation (ontogenesis from selection) but the niche construction perspective can apply to other dichotomies as well : (1) the genotype-phenotype distinction (2) the separation between development and the developmental environment (on developmental or evolutionary time-scales), etc. As for (1), if the phenotype has a characteristic time comparable to that of the genotype (on a given time scale of interest), the genotype-phenotype separation no longer holds. This can be the case for instance in evolutionary cultural studies, where cultural variants (*e.g.* dairy farming) can last for millennia, letting enough time for "genes for" culture (not genes for digestion here) to evolve as well, or in the case of oxygen enrichment examined above. As for (2), if, say, ontogenesis modifies the developmental environment on an evolutionary time-scale, we have one more way in which ontogenesis can influence evolution (and possibly selection).

Environment or phenotype

The analytic difficulty when comparing selection and niche construction, is that there is no difference in nature between a phenotype and a selective environment : a phenotype is a modification of the environment that awards some fitness to a gene, thus this modified part of the environment impacts the selective process undergone by the gene:

$$w = s(p, E)$$

where the phenotype p is environmental in nature (s is the selective function). If the selective environment was defined as everything in the environment that affects the (differential) replication of the gene, ontogenesis, if not neutral, could always be seen as a modification of the selective environment. This is as true within the classical selectionist scheme (even with frequency-*in*dependence), as within niche construction theory[1].

The difference between the phenotype and the so-called selective environment lies only in the time-scales we usually attribute to the phenotype's dynamics (*i.e.* gene's effects on the environment) as compared to the selective environment's dynamics (*i.e.* environment's effects on gene's fitness) : in classical selectionism we assume that these dynamics are separated. Actually, one of the main endeavours of the selectionist theorist consists in delineating a phenotype/environment boundary that enables her to apply this time-scale separation: rather than everything in the environment that differentially affects the replication of the gene, the "autonomous" selective environment is this specific part that is not affected by the ontogeneses in presence (for instance, the "autonomous" selective environment is that part of the environment which determines the pay-off matrix in frequency-dependent selection).

Because of these ambiguities, we avoided to cast the problem in terms of (modified) environments and rather used a time-scale separation criterion to distinguish the classical selectionist scheme from niche construction theory. We will come back on the issue of "selective environment" in section 4.2.

1 Our account departs from Brandon's account. In his definition, Brandon shortcuts ontogenesis: "The selective environment is measured in terms of the relative actualized fitnesses of different genotypes across time or space." (Brandon 1990, 1992, Brandon & Antonovics 1996:chap.10). "Selection occurs when differential adaptedness to a common selective environment leads to differential reproductive success." (Brandon 1992).

Space *vs* time

In our view, niche construction can be a valid theory even in mean field situations. Space is not intrinsic to the theory (the word "environment" appears more than hundred times in OLF's book[1], but "environment" is a spatial concept only in the sense that it invites us to presume a separation between individual's internal and external compartments, not in the sense of any distance between individuals). Though not intrinsic, space is of primary importance, however. Here, we mean space as limited dispersal, which leads to viscous populations. It can be thought in parallel as limited diffusion of the extended and posthumous phenotypes. Limited dispersal results in lineages being correlated (through time) with particular places (Lehman 2009:139). (This in turn results in spatial autocorrelations of genes, which can enhance kin selection, see Van Baalen and Rand 1998.) If interactions between individuals and with the environment have limited spatial ranges, an individual that locally modifies the environment can, *ceteris paribus*, more easily differentially affect the fitness of its descent (Lehman 2007:2), than in mean field situations. The geometry of space is decisive here : fractal geometry, for instance, leads to more confined interactions (*e.g.* Wiens and Miles 1989, Sugihara and May 1990). Space, thus, (and it was somehow expected) is of primary importance for the evolution of the spatial *but also* temporal extensions of phenotypes. In this respect space can influence the time-scale separations of the considered processes, as it has been shown, in ecology, by infinitely delayed competitive exclusion in viscous populations (Hurt & Paccala 1995, cf. this thesis, chap.1:3.1).

4. Problems of niche construction : adaptation, externalism

Now that we have discussed what niche construction is, we are going to examine two constructionist issues : the redefinition of adaptation (to an environment) by the constructionists, and in which way the niche constructionism departs from the selectionist externalism.

4.1 Adaptation

One main goal of the constructionist framework is to "rethink adaptation" (Day *et al.* 2003, see also *e.g.* OLF 2003:16-19,374-376, Laland 2004:316). This is ambitious, as adaptation is probably one of the most central concepts of evolutionary biology. Here we discuss adaptation *sensu* the fact that an entity is adapted (to the environment), and not the dynamical process of getting adapted.

Concepts of adaptation

Classical selectionism recognizes two different kinds of features that can possibly enhance the fitness of organisms (or rather phenotypes) : (1) features that have been shaped by selection throughout the history of the lineage, and (2) features that have not been shaped by selection. Darwin (1859:197) and Williams (1966:v,4), for instance, considered only the first as adaptations, the second being referred to by Williams as (sometimes incidental) effects

1 This represents, by the way, an occurrence 30 % greater than for the word "organism" (ca. 73 occurrences), and 10 % greater than for the word "gene" (ca. 88 occurrences).

(1966:v,13). By contrast, Bock (1979:39) considered that both were to be counted as adaptations, following the vernacular intuition of the word that something is adapted to a role if it fulfils its role, whatever the origin of this fit (Endler 1986:47[1]). This is also the "currentist" concept of fitness defended by Reeve and Sherman (1993), who argued that the usual "historical" concept of adaptation, equating it with direct effect of selection, misses the whole research program of behavioural ecology. Throughout his book, Williams (1966) has been very severe with regard to the conflation of the first and second meanings. His book starts with these words : "Evolutionary adaptation is a special and onerous concept that should not be used unnecessarily, and an effect should not be called a function unless it is clearly produced by design and not by chance." (1966:v, see also *e.g.* 4,8-9). Williams refers to chance, here, because Lamarckism is dismissed, and no other process than natural selection is supposed to enhance fitness. To clarify the debate, Gould and Vrba (1982:6) proposed to still name adaptations the features shaped by selection, and to coin a new word, exaptation, for "unselected, but useful" features.

Thus, classical selectionism recognizes two different ways towards the "fit" of an organism (or phenotype) to its conditions of life : natural selection (adaptation), and chance (exaptation)[2]. The "fit" is measured in terms of (absolute) fitness[3].

In niche construction, the vocabulary is somewhat richer. Following Bock (1980), Odling-Smee (1988:98) calls a "synerg" the matching condition between a organismal feature and an environmental factor (see also OLF 2003:41,43, Laland *et al.* 2003:118). In some instances, we find the terms "synergic match" (Day *et al.* 2003:82), "synergistic relationships" (OLF 2003:43), "hand-in-glove fit" (Laland and Sterelny 2006:1758), "dynamic complementary match" (Day *et al.* 2003:93, or only one of these two adjectives : OLF 2003:50,164,240), "dynamic adaptive match" (OLF 2003:3,376), "evolving match" (OLF 2003:18), "evolving complementary match" (Day *et al.* 2003:80), or just "match" (OLF 2003:48-49:fig.2.1,290, Laland 2004:321,322, Laland and Sterelny 2006:1758, Laland *et al.* 2008:198), to describe the match between an organism and its environment. We gave some details on the occurrences, here, to show that this terminology is not anecdotal. We find the

1 We do not follow Gould and Vrba's (1982:4) account here, to whom the vernacular meaning refers to "*ad + aptus*, or towards a fit (for a particular role). When we adapt a tool for a new role, we change its design consciously so that i will work well in its appointed task.". It seems to us that it is only one side of the vernacular coin.

2 Our argument here is different from Odling-Smee's finding (1988:82) : "The synthetic theory currently assigns a dual role to the environment. One role is explicit, pragmatic, and obvious. It is assumed that the environment is the sole source of natural selection. Its second role is implicit, philosophical, and far less obvious. Natural selection is assumed to be the only force capable of altering gene frequencies nonrandomly, and therefore to be capabe of directing evolutionary descent down nonrandom paths.".

In our view, natural selection is not the only "force" capable of directing gene frequencies (as mutation pressure could be considered too), but the only "force" capable of directing gene frequencies *with respect to fit* (see section 4.2 for a discussion of natural selection as a force).

3 As regards adaptation, frequency-dependence is a complicated issue, because the selective process makes the selective environment vary at the same pace than does the population. Strategies are not always linearly ordered in terms of success : *A* might win on *B*, *B* on *C*, and *C* on *A* (for such rock-paper-scissor games in the field see *e.g.* Sinervo and Lively 1996). Here, we can rescue the concept of adaptation by narrowing the time-window on which we investigate whether, given similar environments, absolute fitness has increased in the population.

term "adaptation" too, and it refers, sometimes explicitly, to Williams' sense (*e.g.* OLF 2003:41,49,370, Laland and Sterelny 2006:1756), though we found it used in the sense of "fit" rarely (*e.g.* OLF 2003:3,284)[1].

Construction towards fit ?

The niche construction perspective on fit is rather unusual : "[T]here are two routes to the fit between organisms and their environments: (1) organisms may, as a result of natural selection, evolve characteristics that render them well-suited to their environments; or (2) niche-constructing organisms may change their environments *to* suit their current characteristics." (Day *et al.* 2003:81, my emphasis on the problematic "to" ; see also *e.g.* OLF 2003:18,43,240,290,375,376, Laland 2004:321, Laland and Sterelny 2006:1758,1759, Laland and Brown 2006:95). Or, in a nutshell : "Adaptation depends on both natural selection and niche construction" (OLF 2003:3:fig.1.1). Here "adaptation" is probably a misnomer for "fit", as the authors are coherent using Williams' (1966) sense in the rest of their book (OLF 2003). This perspective stems from Lewontin's emblematic sentence : "Organisms do not adapt to their environments, they construct them out of the bits and pieces of the external world." (1983:280, quoted in OLF 2003:17, we find a similar sentence in Lewontin's commentary on the cover of the book). To OLF, indeed, the way classical selectionism looks at adaptation is a "problem" and a "deficiency" (2003:375). Lewontin himself proposed to replace the "metaphor of adaptation" (1983:280) by the "metaphor of construction" (1983:282). So, is niche construction a third[2] way toward fit, in addition to chance and natural selection, or is it reducible to one of them ?

Let's take a look again on OLF's (and Lewontin's) examples of organism-environment fits possibly attained by construction. We find : spiders adapting to their webs *or* constructing webs suited to them (OLF 2003:17), earthworms "weakening [soil] matrix potentials and mak[ing] it easier for them to draw water into their bodies" rather than undergoing adaptation to life on land of, for instance, their "freshwater" kidneys (OLF 2003:374-376), and probably most of the examples of the OLF's Chapter 2 (OLF 2003:50-115), some of them having already been given above (section 3.7). As for Lewontin's examples, we get : "ants mak[ing] fungus farms, trees spread[ing] out leaves to catch sunlight, (…) beavers rais[ing] the water level of a pond, (…) white pine (...) creat[ing] a dense shade that prevents its own reseeding"

1 The ambiguity of the niche construction framework about adaptation is exemplified by this quote :

"In summary, if ''adaptation'' means the asymmetric accommodation of a lineage to its environment, then niche construction does not cause adaptations (sensu Williams 1966) in the niche-constructing lineage. (Niche construction may cause adaptations in this sense in other lineages: domestic mice are adapted to human-caused changes in their environment.) But although niche construction may not explain adaptations in this narrow sense, it does explain organism-environment matches." (Laland et Sterelny 2006:1759)

First, we can notice that niche construction does not cause adaptation of mice to human-caused changes : *selection* does. Second, the "organism-environment match" is not, in our view, proven by the paragraphs preceding the quote.

2 A third route, and not a "second route", as OLF put it (*e.g.* 2003 :43,240,290,376). Of course it could be argued that chance is not a route, but a drift. This issue is not very important here, what matters is not to forget chance, and not to award niche construction fits that are due to chance.

(1983:281[1]) (in the last example we have negative niche construction).

As we already mentioned (section 3.7) the given examples can be interpreted in terms of intra or inter-genomic coevolution, which is acknowledged by OLF : “Although it is not clear that all of these adaptations are actually evolutionary responses to prior niche construction, it is likely that many of them are. This means that it may frequently be appropriate to consider evolution as a process in which environment-altering traits coevolve with traits whose fitness depends on alterable sources of natural selection in environments.” (2003:113). According to this interpretation, niche construction is not at all a supplementary route towards fit, but a phenotypic part of a classical selective process. Thus, rephrased in genetic terms, the niche construction perspective on fit (given above) reads : “There are two routes to the fit between a gene and its environment: (1) the gene may, as a result of natural selection, evolve a classical phenotype (*sensu* internal to the organism, if any) or (2) the gene may evolve an extended phenotype.”. Well. This is much less unusual.

Even if we consider the particular case where the niche construction phenotypes at the origin of the subsequent selective process have not been shaped themselves by prior natural selection (OLF 2003:19,372, section 3.9), the classical selectionism applies[2] : there is indeed no impossibility of coevolution between traits that are effects (*sensu* Williams 1996:v) and other selected traits. Here the coevolution would be asymmetrical as effects are by definition non-selected traits, but we still do not have any new route to fit.

What about non-genetic niche construction (if any) ? Even in this case, we do not get any insight that niche construction, and not classical adaptation or chance, leads to fit. If niche construction arises from developmental noise (OLF 2003:372), it has to be shown how noise can lead, except by chance, to fit. If niche construction arises from acquired characteristics, from instance from learned behaviours (*e.g.* OLF 2003:21,372), it has to be shown how these acquired characteristics enhance fit, without the capacity of acquiring such capacities (*e.g.* the capacity to learn) having been itself shaped by natural selection (Sterelny 2005) (section 3.9). OLF themselves seem to accept that the path towards fit through acquired characteristics is due to natural selection, as they write : “Niche construction (…) must be directed by semantic information whose structure and content is the result of prior natural selection.” (2003:176:table 4.1)[3].

We can work out the earthworm example to give a dichotomous key of what is at stake here. Earthworm is a famous example of niche construction (see *e.g.* OLF 2003:11,160,291,375, Laland 2004:319-321, Laland & Brown 2006:99, Laland & Sterelny 2006:1754,1758-1760, Laland *et al* 2009:199, Laland *et al.* 2008:552,554,560), it deserves a famous discussion. First, we observe that earthworms modify the edaphic environment and make it more “aqueous”. Only better : this suits the worm (Darwin 1881:310, Turner 2000). Has there been any selection for modifying the soil and making it more aqueous, for instance, by mucus

1 Here we give only examples of organisms altering the external world, but Lewontin sees three other routes towards construction : to “determine what is relevant, (…) [to] transduce the physical signals of the external world, (...) [to] create statistical patterns of environment different from the patterns in the external world” (1983:281). See section 4.2.

2 If, of course, ontogeny and selection are not entangled.

3 OLF would probably deny that this sentence pleads for a supremacy of natural selection, given their argument on reciprocal causation. We already examined this argument (section 3.9).

secretion ? If yes : we have a case of classical natural selection (Williams 1966:19[1]). If not, the constructing activity is a “mere effect” ; then, was there any other reason (than the already discarded natural selection) to expect that this constructing “mere effect” would be beneficial to the worm ? If not : fitness enhancement results from mere chance (for instance, it is usually assumed that mutations are random with regard to fitness, in the sense that knowing the fitness of a trait is supposed to tell us nothing about the probability of the corresponding mutation(s), if any[2]). If yes : the new way towards fit has to be worked out, because it sets the stage for a scientific revolution.[3]

Unfortunately, we have not been able to find a single clue that niche construction leads to fit by other ways than natural selection and chance in OLF's writings. By the way, OLF themselves consider that niche construction can be positive (enhancing fitness), but also negative (decreasing fitness), thus niche construction sometimes generates a mismatch between the organism and the environment (OLF 2003:47-50). Niche construction should thus be a route towards non-fit as well. One more time, we do not know of any process that can give us an expectation of the sign of a new niche construction activity, and thus an expectation of the impact of niche construction on fit once selection is discarded (we consider chance does not give any expectation of the sign). If we use our rephrasing of niche construction in terms of time-scale separations, we can say that we have no clue that the non-separability of ontogenesis and selection should lead to fit (recall that fitness is still defined in this case)[4]. Neither do we have any clue that, when ontogenesis is separable from selection,

1 In this section, Williams discusses the level of selection : individual or populational.

2 To be precise, we can imagine non-random mutations with regard to the phenotypic dynamics (hence inheritance of acquired characteristics), which could nevertheless be random with regard to fitness (hence non-Lamarckism).

3 In the following quote Laland *et al* (2005:41) offer a subtle discussion of the distinction between effects and adaptation :

“If the only feedback to an organism from a niche-constructing activity were due to effects on selection of the genes that underpin the activity, then whether the character is an adaptation or effect is of paramount importance, since the difference between these impinges on survival value and reproductive benefits of the character. But, as all three commentators seem to accept, this is not the only form of feedback from niche construction. Such activity frequently also modifies selection pressures acting on other aspects of the phenotype, in the same or in descendent populations; for this second kind of feedback the distinction between adaptation and effect is irrelevant. One of the contributions of the niche-construction perspective is to focus on the symmetry between these rather that their sequential nature, which is the old way of thinking about evolution (Lewontin 1983).”

By contrast, we consider that for this second kind of feedback, there is, first, no feedback (since the modified pressures act on other aspects of the phenotype, that is, given the first sentence of the quote, on other genes). Second, the distinction between adaptation and effect is still relevant, and activities of this kind are, indeed, effects.

4 The claim is quite explicit here : “The focus [of ecological developmental biology] is the ability of developing organism to sense cues from its environment and to modify its development to become more fit in a particular habitat.” (Laland *et al*. 2008:549). We strongly doubt that such examples of this “ability to sense cues” are not due to chance or natural selection. Gould and Vrba (1982:592), for instance, give some examples of fit without selection : “Many sedentary marine organisms, sponges and corals in particular, are well adapted to the flow regimes in which they live. A wide spectrum of 'good design' may be purely phenotypic in origin, largely induced by the current itself.”. Here, it can be argued that either there has not been selection for the response to the current (or there cannot be, in which case fitness is

extended or posthumous phenotypes should lead to fit, except by chance or selection.
In conclusion, the claim that niche construction is a new route to fit should be entirely avoided, or clearly labelled as pure speculation. (This is not pejorative.)

Note :
As for history, even Julian Huxley was, contrary to Darwin, insensitive to adaptation, *sensu* fit (Ruse 1992:79). As for us, we remain *a priori* agnostic : unless a proper metric is defined for the "match", enabling to compare possible and realized states, we do not see why we should consider that organisms match or do not match their environment[1].
Throughout our discussion, we have considered that fit is given in terms of fitness. This is in accord with OLF's use of "match", also referring to fitness (*e.g.* 2003:47-50). We could imagine, however, other currencies, maybe better suited for constructionist or interactionist views. For instance, the minimization of some energy would give the degree of match between a living system and its environment by the degree of minimization of the interaction's energy (in development or evolution). Theories of this kind could or could not relate much to Darwin's work. We mention this perspective only as a theoretical possibility : until a proper state phase is defined to compute the considered energy, the perspective remains metaphorical (Van Valen 1991 goes in this direction, see also Bouchard 2007).

4.2 Back to the basics : is selectionism an externalism ?

OLF (2003:18) following Lewontin (1983:282) oppose the selectionist scheme as an externalism involving unmodifiable selection pressures imposed by the "external environment" (*e.g.* 2003:10,131,419, "external" means here external to the organism). Lewontin's metaphorical equations (given above in section 3.1, repeated in section 4.2), for instance, characterizing the selectionist scheme, have organism and *environment* as variables. Here we aim at specifying in which sense the selectionist scheme is externalist, and in which sense constructionists or interactionists views depart from it (if ever they do).

Historical perspectives

Darwin himself did not state clearly his scheme in an externalist way[2]. We have not been able to find the word "environment" a single time in the diverse editions of *The Origin* (1859-1876). Neither did we find the phrases "selection pressure" or "selection force", which do not, to our knowledge, exist in his writings. What we found, by contrast, are the concepts of organisms "adapting to" (*e.g.* 1859:82) (or being modified by, *e.g.* 1859:4,10) their "conditions of life" or "existence", of "places in the economy of nature" to be "filled up" (1859:81), of organisms being "fitted for their places in nature" (1859:88, 199) or "fitted for

irrelevant), and fit, if any, is due to chance, or there has been selection.

1 Subjectivity is important here, because if we lack imagination, we will not envisage other possible organism-environment relationships where the match could be much, much, higher.

2 This is somehow acknowledged by Laland *et al.* (2008:554) : "Although Darwin recognized organisms as constructors of their environment, and championed some marvelous examples of niche construction (e.g. earthworms, coral), his postsynthesis legacy became a view of organisms as passive objects molded by the external force of selection."

We are not sure, however, that Darwin would have been a constructionist in his time.

(...) different habits of life" (1859:183). Significantly, Darwin's work is mostly stated in terms of "laws" (*e.g.* 1859:v-x, 489-490), the highest, in his view, being "the law [of] Conditions of Existence (...), fully embraced by the principle of natural selection" (1859:206). "Conditions of existence" might seem close, though not synonymous, to our concept of environment[1], but other concepts such as "habits of life" seem a bit less environmental.

Spencer, now famous mostly for having coined the sentence "survival of the fittest" to describe natural selection (1864:444) but who has been more influential in his time, is by contrast, according to Godfrey-Smith (1998:68), a great externalist. Spencer, indeed, speaks of selection in terms of "fit" of organisms to their "environments" (1886:42). He specifies, however, that fit is "a figure of speech" that has not to be understood as the fit of "a glove [to] a hand" but in terms of what he, and we, now call fitness (1886:42). In his view, the environment is constituted of "universally-present" "matters and forces" (1886:47).

Today, it is commonplace to consider that selective "forces" or "pressures", whatever they mean, stem from environmental factors. To Godfrey-Smith for instance, "In adaptationism[2] the externalist pattern of explanation is displayed more clearly than it is anywhere else. Adaptationims seeks to explain the structure and behavior of biological systems in terms of pressures and requirements imposed by the system's environment. Biological structure, or some very significant portion of it, is understood as an adaptive response to environmental conditions." (1998:32, see also 1998:142, or *e.g.* Williams 1992:484). Following Lewontin (1983), the constructionists regret that in the standard view, "The adaptations of organisms are treated as consequences of independent natural selection pressures moulding organisms to fit pre-established environmental templates." (Odling-Smee 2009:70, see also *e.g.* Day *et al.* 2003:81, Laland 2004:315, Laland *et al.* 2007:54, Laland *et al.* 2008:554, Laland *et al.* 2008:197).

So, what is the "environment" here? How is it "external" to the organism, or, more generally, to the living system? Where do the "selective forces" come from?

Selective laws and selective forces

Selective "forces" or "pressures" are metaphors borrowed from physics. In physics, matter and energy, and the resulting forces (or potentials), are variables, they are spatialized, that is, they have spatial coordinates. By contrast, laws and other invariants are, by definition,

1 Darwin aims here at combining both Geoffroy's and Cuvier's theories into a single theory: Geoffroy's idea of the unity of type was, in Darwin's view, to be understood by common descent, and Cuvier's principle of conditions of existence was to be understood by natural selection (Darwin 1859:206, Ovspovat 1981-1995:150). The following quote of Cuvier helps to see the link between the "conditions of existence" and the environment:

"L'histoire naturelle a cependant aussi un principe rationel qui lui est particulier, et qu'elle emploie avec avantage en beaucoup d'occasions; c'est celui *des conditions d'existence,* vulgairement nommé *des causes finales.* Comme rien ne peut exister s'il ne réunit les conditions qui rendent son existence possible, les différentes parties de chaque être doivent être coordonnées de manière à rendre possible l'être total, non-seulement en lui-même, mais dans ses rapports avec ceux qui l'entourent, et l'analyse de ces conditions conduit souvent à des lois générales tout aussi démontrées que celles qui dérivent du calcul, ou de l'expérience." (1817:6, Cuvier's emphasis ; on this subject see Huneman 2006, 2008:341-363).

2 Godfrey-Smith speaks in terms of "adaptationism" rather than "selectionist scheme", but this does not matter if we consider selection as the only way towards adaptation.

invariant under translations in space (at a given scale), and do not have such spatial coordinates. Thus, if there were such selective forces, they could have spatial coordinates and stem "from the outside" of a living system (*e.g.* Spencer 1886:48[1]), by contrast with the corresponding selective laws (*i.e.* the selective invariant in our terminology) that could not. Actually, Endler has shown how misleading these metaphors can be (1986:29-33): for instance, if the selective forces were to be applied on gene frequencies, it would seem hard, at first sight, to make sense of what the corresponding "mass" of the set of frequencies would be. It is, in our view, easier to think in terms of invariants (labelled as "selective" if there is a selective process) and variables, that can be either environmental or biotic variables.

Selective invariants, such as the so-called "selection pressures" which can be seen, *sensu* selection coefficients, as short term invariants, are neither "pressures" nor "forces", they are laws that describe the interactions between living systems and their environment. They have no spatial coordinates, and strictly speaking, they are neither internal, nor external to a living system. They are "external" to the living system only in the sense that they are invariants, while the living system is a variable. Here we come back to Darwin, following Cuvier's use of the word "principle" and Whewell's appeal to "general laws" (Darwin 1859:ii), who casts evolutionism in terms of laws. (Lewontin's concept of constraints, in the quote given below, seems similar, though the invariant could be different.)

On the other hand, the invariants, that describe the interactions between the variables, can describe asymmetric forcings between variables. If some environmental variables have autonomous dynamics, that is, if their dynamics are not influenced by biotic variables (*i.e.* the effects of the biotic variables on environmental variables are time-separated from the environmental variables' dynamics), the intuition that some part of the external environment exerts a "force" on the living matter, but not the other way around, is legitimate (though it is not, strictly speaking, a force but rather a forcing). For instance, we classically consider that Earth exerts a gravitational force on living matter, but we seldom consider the reciprocal. Now, classical selectionism assumes a separation between ontogenesis and selection, that is, in particular, that phenotypes do not modify the selective environment. Hence, the selective environment *forces* the living's dynamics, and classical selectionism is an externalism. Here we come back to Spencer's intuition that evolution is forced by, or undergoes a "force" from,

1 "Obviously the most general trait is the greater amount of change wrought on the outer surface than on the inner mass. In so far as the matters of which the medium is composed come into play, the unavoidable implication is that they act more on the parts directly exposed to them than on the parts sheltered from them. And in so far as the forces pervading the medium come into play, it is manifest that, excluding gravity, which affects outer and inner parts indiscriminately, the outer parts have to bear larger shares of their actions. If it is a question of heat, then the exterior must lose it or gain it faster than the interior; and in a medium which is now warmer and now colder, the two must habitually differ in temperature to some extent – at least where the size is considerable. If it is a question of light, then in all but absolutely transparent masses, the outer parts must undergo more of any change producible by it than the inner parts – supposing other things equal; by which I mean, supposing the case is not complicated by any such convexities of the outer surface as produce internal concentrations of rays. Hence then, speaking generally, the necessity is that the primary and almost universal effect of the converse between the body and its medium, is to differentiate its outside from its inside. I say almost universal, because where the body is both mechanically and chemically stable, like, for instance, a quartz crystal, the medium may fail to work either inner or outer change." (Spencer 1886:48)

the environment (*e.g.* Spencer 1886:49[1])[2].

In conclusion, selectionism is externalist in the sense that there is an asymmetry in reciprocal influence between environmental variables and biotic variables, which entails non constructionist explanations. Environment here has to be defined as a set of *variables* that "can be described independently of the properties of the organic system" (Godfrey-Smith 1998:151). By contrast, selective invariants are neither environmental nor internal to living systems. This is why, in section 1.2, we defined the different explanatory regimes (internalism etc) according to the localization of input *variables*.

Back to Lewontin's equations

As we already noticed (section 3.1) Lewontin proposed to characterize externalist explanations as a pair of differential equations "describing the changes in organisms O as a function of organism and environment E (…) and the autonomous change of environment" (1983:282). Externalism is given by :

$$\frac{dO}{dt} = f(O, E)$$

$$\frac{dE}{dt} = g(E)$$

while, by contrast, constructionism is given by :

$$\frac{dO}{dt} = f(O, E)$$

$$\frac{dE}{dt} = g(O, E)$$

These metaphorical equations are a bit insufficient to characterize his view, however, in the sense that constructionist explanations, thus defined, can be externalist in some respects. Indeed, when writing dE/dt=g(O,E), Lewontin does not specify whether there is or not an autonomous forcing (see glossary) in the dynamics of E (such as an autonomous supply rate) that is not modifiable by O. If these equations are to describe dissipative systems (for

1 "If, now, inorganic masses, relatively so stable in composition, thus have their outer parts differentiated from their inner parts, what must we say of organic masses, characterized by such extreme chemical instability?—instability so great that their essential material is named protein, to indicate the readiness with which it passes from one isomeric form to another." (Spencer 1886:49)

2 There is a another, close but not identical, way to consider that evolutionism (not selectionism) is an externalism (or not). It comes from the consideration of evolution of different lineages put in similar environments (and the possible evolutionary convergences), and from the consideration of radiations of a single lineage in different environments (and the possible evolutionary divergences) (see the section on Grinnell and Elton, this thesis, chap.1). If the lineages never constrain evolution under natural selection while environments do (for instance if mutation is non-limiting), selectionism will be thought of as an externalism. However, lineages sometimes do constrain evolution: for instance, depending on their location in the adaptive landscape, lineages will not always climb the same adaptive peak (if any), or may even not climb any peak at all (selective stasis) because of developmental constraints (*sensu* Gould and Lewontin 1979:594-597). Here, we would have former lineage properties that would (partially or totally) explain current lineage properties. Thus, depending on focal cases, evolutionism could be sometimes internalist. Dismissing such internalist explanations amounts to considering that biotic variables exert negligible influence on their own dynamics compared to the influence of environmental variables.

instance, if O has any death rate), such an external forcing is expected to take place for the system to somehow maintain. Thus, the apparent causal closure between O and E in the metaphorical equations will be broken in real equations, contrary to OLF's intuition on thermodynamics discussed above (section 3.2).

Then, Lewontin gives a thought-provoking account on evolution under construction, which is worth quoting entirely: “The error is to suppose that because organisms construct their environments they can construct them arbitrarily in the manner of a science fiction writer constructing an imaginary world. The coupled equations of coevolution of organism and environment are not unconstrained (...) Some pathways through the organism-environment space are more probable than others, precisely because there are real physical relations in the external world that constrain change. Where there is strong convergence is in certain marsupial-placental pairs, and this should be taken as evidence about the nature of constraints on development and physical relations, rather than as evidence for pre-existing niches.” (1983:283).

Here, we get Darwin's intuition of evolutionary laws, *contra* Spencer's intuition of external forcing.

Certainly, the key is to know what O and E should mean here. Theoretically, in some cases it will be possible to change O and E in Lewontin's equations to get an understandable externalist account (*i.e.* extended phenotype perspective), where the effects of one variable on the other will be ignored (that is, separated), and Lewontin's “constraints” will reduce to empty niches forcing selection. In other cases, such change of variables will not be possible and tracking the interaction will show necessary (*i.e.* niche construction perspective).

Constitutive *vs* causal construction

Lewontin sees several ways for organisms to construct their world: “Organisms determine what is relevant. (…) Organisms alter the external world as they interact with it. (...) Organisms transduce the physical signals of the external world. (...) Organisms create statistical patterns of environment different from the patterns in the external world.” (1983:280-281). To Godfrey-Smith (1998:144-151), Lewontin conflates two different senses of construction: a “literal causal sense, and a constitutive or ontological sense” (1998:144). In the causal sense, organisms alter their external environments, they construct their world by intervening on it. In the ontological sense, organisms define what their relevant or perceived environments are; they modify their perceived world by undergoing internal change (1998:146).

As for evolution, Godfrey-Smith's distinction holds as long as we consider somehow bounded organisms, but vanishes as soon as we embrace a gene-centrist perspective (with always extended phenotypes). For in a gene-centrist perspective, we have, say, the gene's sequence on the one hand (for the sake of argument let's suppose the sequence is sufficient as far as evolution matters), and the phenotype on the other hand (we limit ourselves to “active” replicators here). Apart from synonymous mutations, any “constitutive” construction (change in the sequence) will result in a “causal” construction (change in the phenotype), and apart from stochastic events, any causal construction will result from gene's constitution[1]. Genetic

1 In our view, the most similar distinction between the two kinds of construction is between traveling in a

mutation always entails both constitutive and (change in) causal construction. Gene : constitution, phenotype: construction. From the gene's point of view, Lewontin's quote above reduces to: “Genes have phenotypes.”

However, there is an intuition that is worth emphasizing in Lewontin's concept of construction, the intuition of co-definition between the living system and its environment: “To make the metaphor of adaptation work, environments or ecological niches must exist before the organisms that fill them. (...) But what laws of the physical universe can be used to pick out the possible environments waiting to be filled? In fact, we only recognize an 'environment' when we see the organism whose environment it is.” (Lewontin 1983:280). This is both true and untrue. (Here, we gloss over the organism/environment terminology and switch back in terms of genes and selective invariants.) Usually for microevolution studies, we consider that we are able to define a (local) selective invariant describing the interactions between sufficiently close variants, even if we did not observe every variants and their interactions in the field. We assume that small mutations will not qualitatively change the interactions. Local extrapolation enables to recognize empty places in the economy of nature even if we do not see directly any pen pusher filling them. Hence in this case, we can define absolute, not relative, environments. Extrapolation is probably less reliable for macroevolution studies. Here Lewontin is right, and selectionism fails: we discover the adaptive landscape (*sensu* selective invariant) as and when the variants travel through it. (See, however, the discussion by Arnold *et al.* (2001:23,26): while they agree that global landscapes are mainly imaginary, they argue that adaptive landscapes can provide extrapolations of micro to macroevolution. See also the discussion of macroevolution right below.)

Conclusion on externalism

Dynamical invariants describe the interaction between a living system and its environment. They are neither internal, nor external to the system. However, if the living system is the only variable that is modified by the interaction, the environment remaining unchanged, then the environment “forces” the dynamics of the living system, and the environmental variables “explain” biotic variables dynamics (and not the other way around). Classical selectionism, by assuming a decoupling of ontogenesis and selection, supposes that the effects of the biotic variables on environmental variables (*i.e.* phenotypes) vanish between generations[1]. Selection,

reaction norm (changing the phenotype without changing the gene), and traveling in an adaptive landscape (changing the gene). But as far as selection is concerned, there is no qualitative difference between displaying a reaction norm and displaying a particular phenotypic value (which is just a constant reaction norm on usual environmental conditions). Thus, even this distinction does not seem very relevant to us.

1 We depart slightly from Godfrey-Smith here, for whom game theory cannot be said “asymmetrically externalist” (1998:136-7), that is, game theory cannot be said to involve an explicit or implicit denial of an effect of the organic system on its environment (1998:135). In our view, either the “organic system” is the population, and then, it has no “environment” in the dynamical system, and game theory is purely internalist. Or the “organic system” is a given individual. Then, if we assume that development and evolution are two different processes (that is, that copying oneself or dying are not phenotypes), we cannot consider that modifications of the environment happening “merely” by evolution of the population count as individual modifications of the environment, hence the individual environment is never modified by individuals and game theory is purely externalist (this does not hold if we do not distinguish

the result of the interaction of the living system with its environment, is “forced” through generations by the environment. In this sense, classical selectionism is an externalism.

By contrast niche construction, *sensu* ontogenesis-selection entanglement, entails that the modifications of the environment have a time-scale comparable to that of the selective process, and thus, that on the selective time-scale, the environment is modified. Whenever there is environmental selective forcing, it does not have enough time to act upon the living's dynamics.

Two concepts of environment have been met : the absolute concept (that is, the environment is defined without respect to the system, let apart boundaries), and the relative concept (the converse). In our view (and Godfrey-Smith's 1998:152), only the absolute concept enables to commensurate different living system's environments, their modifications, their influence on the living system, etc. Moreover, the environment should have the same nature than the living system, that is a – possibly constant – variable, and not an invariant.

A strategy to save externalism is to delineate the living systems in such a way that they are the only variables modified by the interactions with the environment (Godfrey-Smith 1998:48)[1]. The extended phenotype perspective illustrates this strategy with respect to development : the phenotype encompasses all the features modified by the interaction between a gene and its environment. The posthumous phenotype perspective extends the extended phenotype on time-scales longer than single generations, possibly selective time-scales.

There is a strong similarity between organism-centered construction and gene-centred extended phenotypes: both tend to scuttle the organism/environment delineation. Both recognize the same fact: organisms' environments are modified. There is a strong dissimilarity between the two perspectives however. The extended perspective assumes that taking as much environment as possible to save externalism will not matter much as for the dynamics, while the organism-centered constructionist perspective does not. The fact that external constructions do not have the same dynamics than internal construction (as for death, decay, etc) pleads for the constructionist perspective. Even if in this paper we have been arguing that we should not give up the externalist gene-centred perspective for wrong reasons (such as “astonishing” examples of intra- or inter-genomic coevolution), it is very well possible, in our view, that the gene-centred perspective can show insufficient. In the same way that the first replicating entities set the stage for selection, it is possible that the first organisms set the stage for new dynamics (here we come back to Laland's intuition in the quote given in section 3.5[2]). By new dynamics, we mean possibly not only new selective dynamics, like the selective dynamics at the gene level described in Laland *et al.*'s 1999 selectionist model, or like possible selective dynamics involving inheritance and selection at the organism level (or above: Bouchard 2008). What these dynamics can be, we leave it to reader's imagination. (For the moment.)

development and evolution).

1 The environment is co-defined, here, in the sense of the delineation between the inside and the outside (not so much in the sense of factors that are relevant).

2 “In my terms, there are two processes in evolution, natural selection and niche construction. There is a power and utility to regarding the gene as the unit of selection, but equally there is value to seeing the organism as the unit of niche construction.” Laland (2004:324).

5. Other alternative evolutionary biologies and niche construction

Apart from the revision of the selectionist scheme and of the concept of adaptation that we examined at length, niche construction theorists have assigned to niche construction several other implications on evolutionary biology. Here we aim at reviewing them in a condensed way.

5.1 The "new" *explanandum*

The most obvious implication of niche construction is to change the *explanandum* of evolutionary biology: now environmental states, as well as genes or strategies, are variables to explain (*e.g.* OLF 2003:171, Lehman 2007). Of course, from the gene's point of view, there is not much difference between investigating the phenotypic state and the environmental modification's state[1]. But by putting an emphasis on an explicit description of the dynamics of the interaction between a gene (or an organism, in their view) and its environment, niche constructionists depart from the tendency to dismiss ontogenesis in evolutionary studies. Moreover, as many examples of niche construction phenotypes are in fact plastic phenotypes (such as learned behaviors), the emphasis put on ontogenesis resonates with the recent trend to take phenotypic plasticity into account in ecology and evolution (*e.g.* West-Eberhard 2003, Pigliucci 2005, Miner *et al.* 2005, Donohue 2005).

In this respect, and when there is no ontogeny-selection entanglement, the niche construction framework can be seen not so much as a new theory, but as a plea to take phenotypes, extended or not, into account (though the constructionists put their emphasis in terms of taking *organisms* into account, *e.g*. Laland and Sterelny 2006:1752).

5.2 The multiple entanglements

Another implication is to envisage the possibility of multiple channels of inheritance in addition to genetic inheritance, each with its own characteristic time. The mechanisms of nongenetic inheritance range from DNA methylations, cytoplasmic and somatic factors, nutrients provided in egg, to habitat quality and influences of parental behavior on offspring development (these mechanisms are reviewed in Bonduriansky & Day 2009:105:table 1, Jablonka & Lamb 2005, for an analysis framework of inclusive heritability see Danchin & Wagner 2010). Notably, the recent momentum gained by non-genetic (or non-nucleic) inheritance can be seen as a resurgence of a question which is a century old (Sapp 1987).

1 For instance : "(…) by directing so much attention to the adaptations of organisms, and so little attention to the changes caused in environments by niche-constructing organisms, standard evolutionary theory also plays down the consequences of evolution for environments. Environmental change is seldom regarded as another aspect of the expression of biological evolution itself, and is therefore seldom included as part of evolutionary theory. Exceptions occur when environments are artificially restricted to other biota, as in population-community ecology where, for instance, coevolutionary models can be applied. However, as soon as abiotic environmental components are also included, as in process-functional ecology, it becomes difficult for the standard theory to describe environmental change in evolutionary terms." (OLF 2003 :171).

This can be read, without any loss in generality, as a plea to take extended and posthumous phenotypes into account.

Interestingly, multiple inheritances seem to mark a return to Galton's (1897:401) conception of inheritance[1].

Constructionists propose to simplify multiple inheritances into a dual inheritance system with genetic and environmental inheritances, where environmental inheritance does not rely on replicating entities[2] (*e.g.* OLF 2003:12-16, Odling-Smee 2007, Laland *et al.* 2008:553). By contrast, so-called developmental system theorists prefer to take the whole life cycle with all its "developmental resources" as a replicator, without assuming any strong dichotomy between genetic and non-genetic inheritances (Griffiths and Gray 1994:300, discussed in Oyama *et al.* 2003, in particular Griffith and Gray 2003:199 and Sterelny 2003:337). In this paper, we have argued that regarding selection, short lasting posthumous phenotypes (compared to the selective process) should play the same role as classical phenotypes. Certainly, in this case acquired modifications of the posthumous phenotypes can be transmitted down the lineage, but in the same way that acquired modifications of classical phenotypes can be preserved throughout one's life. Thus, in the case of short posthumous phenotypes, to invoke multiple inheritance channels for long-term explanations would be as unnecessary a complication, than to invoke self intra-generational inheritance of one's own phenotype throughout one's life. This said, developmental system theorists explicitly do not focus only on selection (Griffith and Gray 2003:199).

Multiple inheritance will be discussed in another paper, but we can already notice that the time-scales of the various inheritance substrates, and their possible separation or entanglement, should be specified by the multiple inheritance theorists in order to avoid empty claims. Two entanglements are of importance: the ontogenesis-selection entanglement (already discussed here) and the genotype-phenotype entanglement (which will be discussed in a later paper). As for the second, an interesting case occurs when the phenotypes themselves are replicators (*e.g.* Brown *et al.* 2008). In this case, it should be possible to cast the problem in terms of an extended coevolution. "Extended" here means that not only selection will drive the frequencies of each type of replicators, but also, possibly, ontogenesis. In the most complete case, replicators modify each other by their ontogenesis, as with

1 In Galton (1897:401), the deviation *D(t)* from a measured mean *M* in a generation *t* is given by the series (adapted from Sloan 2008) :

$$D_t = \frac{1}{2} D_{t-1} + \frac{1}{4} D_{t-2} + \frac{1}{8} D_{t-3} + ... + \frac{1}{2^n} D_{t-n}$$

Where *D(t-i)* gives the deviation in the ascendancy at generation *(t-i)* (this formula has been worked out by Pearson 1898). Though this equation was meant to explain phenomena of both atavism and persistent inheritance by a proper calculation of the different strengths of ancestry (Sloan 2008), it expresses, in this form, an exponential decay of characteristic time *ln(2)*, which is quite small compared to the characteristic time usually attributed to genetic inheritance. Decaying posthumous phenotypes could fit Galton's formula, if the coefficients were suitably modified, in some complicated, non-Markovian, cases. (We are indebted to Maël Montévil for in-depth discussions on this point.)

2 It is worthy of note, in our view, that for the environmentally inherited materials to be evolutionarily interesting, they should have non-linear autonomous dynamics or non-linear effects on the living system's dynamics. By contrast, for instance, in the simplest case where beneficial materials have linear autonomous dynamics (*e.g.* constant decay) and linear effects on the living system's dynamics, we expect selection for as immediate as possible consumption.

transcription and reverse transtription for instance. How much of biology conforms to this inclusive picture is still to be shown[1].

There is still another entanglement at stake. With posthumous phenotypes, the selective process, *ceteris paribus*, takes more time. This is a supplementary reason, *ceteris paribus*, for this process not to complete its course on a given time-interval. In particular, new mutations can arise in the population before a given posthumous phenotype get entirely selected or deselected. Advent of new variants can modify selection coefficients. This means that niche construction (*sensu* posthumous phenotypes) can favor an entanglement between ecological (selective process) and evolutionary (new mutations) time-scales. Evolution could be a

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1 Godfrey-Smith (2000) remarks that such reverse transcriptions, if probably rare in organic processes, are ubiquitous in cultural processes. He actually speaks in terms of reverse translation, but this does not matter much for culture where there is, at first sight, no separation between transcription and translation. The entire thought experiment is worth quoting :

"I will illustrate the relevant phenomena with a hypothetical example. Hull dislikes fanciful thought experiments, but I hope he will forgive this one, as it illustrates not just the space of possibilities but also some real cases. Imagine there is reverse translation, from protein primary structure to nucleic acid sequence, as well as forward translation. Then we can imagine an organism in which the genetic material initially contributed by parents is in the form of DNA, but once the new individual has used these genes to manufacture proteins, the DNA is broken down. (The proteins regulate their own activities during this middle stage.) At the end of the cycle, new genes for the next generation are made by reverse-translating (and reverse-transcribing) from protein to nucleic acid. In this case, any "allele" exists in two physically different forms through the life cycle – first as nucleic acid base sequence and then as amino acid sequence. Mutations in either form will be passed on.

(…)

Does any of this matter? Reverse translation does not exist. Is there any reason to think about strange cases in which discrete replicators get lost in a sea of causal complexity? Yes, because aside from the need to explore the space of possibilities, these complicated translations and reverse-translations are ubiquitous in cultural transmission.

(...)

Even simpler cultural replicators often exhibit changes of form similar to those in the hypothetical case outlined above. Suppose a bird learns its song from a parent or from other local adult birds. Then the song pattern takes two distinct forms in this process. The young bird acquires its song by picking up sound waves. This results in the formation of neural structures, which persist when the song is not being sung. The song is passed to new birds in the form of sound waves again. We have a causal channel through which the inheritance of variation is possible, but any replicator variant must exists in two physically different forms during the cycle. A mutation at either stage can be passed on. Birdsongs of this kind are not as unproblematic replicators as genes, but they are still good candidates, even though they are of the complicated type illustrated by my hypothetical "reverse-translation" case.

(…)

To the extent that cultural transmission involves a lineage of structures, distinct to some extent from the causal sea surrounding them, where earlier members of the lineage can be causally involved in the production of similar later members, in a way causally responsible for the similarity between them, we have replicators. To the extent that no lineage can be isolated because of constant blending, and to the extent that the similarities between cultural products over time result from a network of dispersed and interacting causal factors, in which all the quirks of human preference and flexibility are involved, we do not have replicators. These are reasons to be skeptical about general replicator- based theories of cultural change, of the type advanced by Dawkins (1976), Hull (1988) and Dennett (1995). » (Godfrey-Smith 2000).

Here, in our view, Godfrey-Smith does not illustrate well his thought experiment, as neural structures are not, runaway from selection, the loose material of living flowing, never quite stable, never quite free, like pillow lavas in an ocean of forms.

As for entanglements, concepts are laid to seek for unexpected or not sought trajectories[1]. Empirical implementations of the "entanglementist" research program should give birth to new concepts also, provided that the invariants and their time-scales are made explicit or explicitly questioned.

5.3 The importance of (not so) rare events

The constructionists put a special emphasis on the role of rare events in evolution: "Even a single isolated niche-constructing event can be evolutionarily consequential. Consider dispersal into a new environment, where descendants of the dispersing organisms will, for multiple generations, "inherit"[2] modified selection." (Laland *et al.* 2008:552, see also, as far as we can merge their views, Griffith and Gray 1994:288). Emergence of a new culture would be a similar example (section 3.9). The constructionists call such events "niche constructing" events because they do not necessarily involve alteration of the genetic materials. "Epigenetic" events or epigenetic mutations could be more general expressions, but epigenetics has a rich story already and Waddington's (1942) original term bears has underwent a shift in the XXth century (Haig 2004). Let's be neutral and call them non-genetic.

Non-genetic mutations can accelerate evolution and enable living systems to "overcome some of the limitations of genetic inheritance" (Bonduriansky and Day 2009:111). This is, after all, a well known role of learning, where successful behavioral variants are kept in mind, to deal with small time-scale problems (see Danchin *et al.* 2008:129), or of some maternal effects that can complement environmental cues to determine behaviors such as, for instance, diapauses in insects (Mousseau and Dingle 1991:514).

However, theoretically such "rare" (or not so rare), sporadic, events can not only act as (non-genetic) novelty inducers, but also change the phase space of development and/or selection. That is, new dimensions in the phase space get relevant and some get irrelevant as for the dynamics ; phase space shifting is a way of expressing a radical change in the

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as far as we know, germline replicators (*sensu* Dawkins 1976-2006) – by contrast with songs. In this respect, neural structures will be more easily thought of as phenotypes of the songs, which are the only replicators at play. A different situation, however, occurs with substrates of human cultural objects : digital objects can be seen as germline replicators, as well as the cultural objets that they record. But in this case, it can be argued that mutations in digital objects (such as crash-disks during thesis redaction) are probably not a driving force of cultural evolution, compared to, say, behavioural mutations. This comes from the fact that digital objects are, for the moment, rather reliable replicators with very low mutation rates. Better examples of such reverse-translation couples could maybe be found in economy, though we did not investigate this way much.

Finally, we quoted also one of the conclusive paragraphs, which does not relate much to the problem of reverse-translation, to show that this thought experiment was not Godfrey-Smith's main point here.

1 We gloss over the "new" trajectories of Laland *et al.*'s (1999) seminal model and its descent in OLF's (2003) book, which result merely from changing the type of natural selection. Something more unexpected can probably be derived from niche construction.

2 The quotation marks are of importance here. The descent inherits the new environment only if we compare two populations in different environments, otherwise, there is no variability and thus, no heritability.

developmental/selective process[1]. In this category could fall some of the "dispersal mutations" and "cultural mutations" mentioned above. From the genetic point of view, new parts of the reaction norms get exposed to evolution. This, of course, can favor the non-separability of ecology and evolution, if phase-space shifting is rendered more frequent by niche construction.

Phase space shifting already occurs, however, with classical environmental changes. The reason to invoke niche construction (*sensu* extended or posthumous phenotypes) here, would be to show that such non-genetic mutations are non-negligible phase-space modifiers in the course of evolution. This cannot be done by exhibiting isolated examples, but by integrating them into an "entanglementist" theory. For instance, ideally, a theory of non-genetic mutations would give probability distributions of the expected mutations[2].

5.4 Bringing a new theory of macroevolution

Close to the idea of phase-space transitions, we find the idea of macroevolution. We can define microevolution as the selective process occurring in a given phase space (of traits), while macroevolution occurs when the system changes of phase space, either because of changes in developmental and/or selective environments, or simply in the course of the dynamics, because of critical points in the phase space where (unexpected) pleiotropy occurs or new traits get (surprisingly) evolutionarily relevant.

Changes in phase space, and definitions of the relevant phase space of traits, are questions tackled by the evo-devo framework (see Minelli 2009). Also, as niche construction can lead to changes in the developmental and/or selective environments, it can favour (or not, if counteractive) macroevolution. This is how we read Laland *et al.*'s plea (2008:551) to build bridges between evo-devo and niche construction, to provide evolutionary biology with a theory of macroevolution (partly based on niche construction). By the way, the fact that niche construction deals with the entanglement of ontogenesis and selection makes *de facto* niche construction theory a (new) part of the evo-devo framework. As for now, the theory is in its embryonic stages, that is, the collect of empirical examples – though in evo-devo, some theoretical advances have been met (reviewed in Müller 2007).

1 Of course, a change in the phase space can be subsumed into a broader phase space. The point here is that not all, but not always the same, developmental or selective dimensions are relevant. The question of qualifying or not a given mutation as a "change in the phase-space" or "a move in the same phase space" is a matter of taste and, notably, of theoretical lightness (in particular of dimensional parsimony).

2 This would be also true, of course, of an ideal theory of genetic mutations. This idea comes from the following quote: "This means that, in addition to chance and natural selection, there is a third explicitly recognized source of evolutionary innovation, which occurs when gene-informed, directed, nonrandom, yet novel, acts of niche construction bring about consistent changes in environments" (Laland *et al.* 2008:561). Here we gloss over the fact that natural selection is not, as far as we know, an explicitly recognized source of innovation, and concentrate on the claim that the niche constructing mutations would be both "novel" and "non-random". The question is: non-random in which respect? A theory of epigenetic mutations should answer this question, and in particular the question of (non-)randomness with regards to fitness, if any.

5.5 Epistasis and the rugged fitness landscape

Some genetic interactions (such as underdominance and epistasis) can make the fitness landscape more rugged (Wright 1932:3), that is, with multiple fitness peaks more or less separated by fitness valleys (the impossibility to prove the non-existence of ridges connecting the peaks justifies the fuzzy "more or less" here ; see Whitlock *et al.* 1995:622). Here the landscape is drawn as a genotype-fitness map or a phenotype-fitness map (Whitlock *et al*. 1995:603, for epistasis in genotype-phenotype maps see the review by Phillips 2008:856-859). This issue is closely connected to macroevolution : such ruggedness of the fitness landscape will cause moves in the phase space of traits (or genes), and thus, possibly, (unexpected) changes of the phase space when one dimension of the landscape gets (ir)relevant.

Eventually, too rugged a landscape could prevent consistent evolution under selection. The topology of the genes (*sensu* their structural similarity) and the topology of their fitnesses would not be similar enough to apply gradualism (Huneman 2010). Certainly, selectionism does not require gradualism, but gradualism enhances the relevance of selectionism. Real occurrences of this theoretical possibility, however, are expected to be reduced by the smoothing effect of individual landscape averaging at the population al level, which makes landscapes less rugged (Arnold *et al*. 2001:18,23)

Niche construction (*sensu* extended or posthumous phenotypes) can also lead, as any other phenotype, to epistasis – at least theoretically (OLF 2003:127). Because of phenotypic extension, niche constructing phenotypes can be, probably, more easily influenced by genes in other organisms (conspecific or not) than classical phenotypes. Here too, the possible effects on the fitness landscapes are an entirely new field of investigation.

6. Conclusion

Selectionism involves one necessary and sufficient cardinal condition : a criterion of selection of phenotypes, that is in our case differences in fitness (survival and/or reproduction). This defines a phenotype-fitness map. For the effects of selection on phenotypes abundance at a particular date to be propagated in time, selectionism requires a second condition : heritability of the selected phenotypes (as heritability entails variability, we do not need the classical but redundant condition on variability here). This condition is fulfilled in particular when the selected phenotypes are defined as effects of long lasting hereditary entities (the genes) on the world. This defines a genotype-phenotype map[1]. Last, for the selective process to be the only process at play, selectionism requires another condition : that ontogenesis be time-separated from selection[2].

1 There is a slight, but notable, slippage here, between defining heritable phenotypes as "entities under the partial control of hereditary entities (the genes)", and as "the very effects of genes on the world" (*i.e.* total control).

2 Moreover, for the dynamics of the phenotypes abundances to be consistent (*i.e.* self similar) through time, selectionism requires another condition : that ontogenesis and selection be consistent, if not invariant, through time (we gloss over the theoretical possibility that both ontogenesis and selection be inconsistent but compensate each other). This is achieved when both developmental and selective environments are themselves consistent through time (recall that the other variables in the system, the long lasting hereditary entities, are already supposed to be individually invariant in time). Relaxing this condition is

Niche construction theory, as for its evolutionary part, consists in relaxing the last condition : ontogenesis is no more separable from selection. The relaxation comes from the consideration that genes can have long lasting (posthumous) phenotypes. Tracking the ontogenesis of posthumous phenotypes is the way to incorporate "mere effects" in the selective processes. Niche construction theory, however, is still an instance of the selectionist scheme, as it is built on the two conditions of fitness and heritability[1]. The "symmetry" between construction and selection has to be understood, in our view, in the sense of a time-scale entanglement of these two processes. Niche construction is a "constructionism" in the sense that the environment does not alone force the phenotypic dynamics through selective events, as in classical selectionism, but also does the gene through ontogenetic events (this might seem rather obvious *a posteriori*, but it was not so obvious, in our view, in earlier formulations of the theory)[2]. As for niche construction *qua* an instance of evo-devo, coming back to the importance of the relationships between ontogenesis and evolution can be seen as a resurgence of XIXth century preoccupations (*e.g.* Haeckel 1866, 1895, Sloan 2008, Amundson 2005).

Other relaxations, such as relaxing the time-scale separation between genotype and phenotype, could lead to even more complex pictures, if found in the field. It is a truism to say that time-separations are crucial in dynamical systems, but it is a truism worthy of note. In our view, some hot debates (about the unit of selection, the negligibility of ontogenesis, the need for internalist explanations, to name just those we discussed) could gain from being stated in terms of time-scale separations, because identified claims are easier to discuss, and because they become empirical rather than conceptual issues.

Even though we gave some support to the theoretical possibility of a "symmetry" between construction and selection, we were not able, by contrast, to find any support for the view that construction should lead to fit. In our view, OLF's claim on the two routes (selection *and* construction, in addition to chance) towards fit should be entirely avoided. This claim obscures what niche construction theory is about, that is, time-scale entanglement, and not any organism-environment match.

Despite remarkable efforts of the founding fathers, empirical evidences are still to be found to get a taste of the evolutionary implications of true niche construction. The examples that have been gathered so far can be interpreted in the classical selectionist scheme, for the most part as intra or inter-genomic coevolutive events, as could be interpreted the examples that might be gathered by field researchers following OLF's method for detecting niche construction in the wild (2003:292). To give niche construction theory some support, a special attention should thus be given, in our view, to the empirical investigation of the time-scales of ontogenesis and selection. Given the difficulty to detect natural selection in the wild (Endler 1986:chap.4), it is not clear whether we will ever be able to detect time-scale entanglement, as

common in evolutionary biology, notably because of varying selective environments, such as in frequency-dependence.

1 Here we consider only the part of niche construction theory that is embedded in the definition of niche construction (OLF 2003:419). We gloss over other interesting parts of the theory, such as the definition of couples {organism, environment} as new *explanda* (*e.g.* Odling-Smee 2007, in our view). This will be discussed in a following paper.

2 Here we mean "construction" *sensu* OLF(2003:419) as rephrased by us, where the feedback is primary, and not *sensu* Godfrey-Smith (1998) where there is no such requisite.

it would suppose to first detect the selective process, if any, at play. Empirical detection would be necessary however, to build a true physical theory from niche construction intuitive premisses.

Main point

Ontogenesis is the process whereby a gene modifies its environment. Selection is the process whereby an environment modifies a gene's fitness (*i.e.* its geometrical rate of increase). The distinction between ontogenesis and selection stems from the distinction between phenotype and replication. Embryology is internalist (*sensu* non-externalist constructivist, section 1.2) if the gene "forces" the environment without being itself modified (non-genetic inheritance of acquired characteristics). Selectionism is externalist (*sensu* non constructivist) if the environment "forces" the gene's fitness.

For clarity, we can split Lewontin's system into two systems describing each ontogenesis (o) and selection (s). Thereafter, g means the population vector of individual genes and E the vector of individual environments[1]. We get:

Ontogenesis:

$$E_{t+\Delta t}=o(g_t, E_t)$$
$$g_{t+\Delta t}=g_t$$

Selection:

$$g_{t+\Delta t}=s(g_t, E_t)$$
$$E_{t+\Delta t}=f(E_t)$$

Here the selective function s and the ontogenetic function o are invariant in the dynamics (f is any function describing autonomous environmental dynamics). Moreover, we assume that genes are left unchanged throughout ontogenesis, and that the environment has an autonomous dynamics throughout selection. We intentionally do not distinguish between developmental and selective environments here, in order to avoid any reactivating of the idea (somehow stemming from the usual time-scale separation between ontogeny and evolution) that development and selection occur in two different worlds.

Lewontin's constructivist claim, worked out by Odling-Smee, Laland, Feldman and others, amounts to claiming that the two systems are not separable (*i.e.* same E and g, and similar Δt). Without time separation, we get the following constructive system:

$$E_{t+\Delta t}=o(g_t, E_t) \qquad (1)$$
$$g_{t+\Delta t}=s(g_t, E_t)$$

where forcings have been removed (but partial forcings can remain, hidden in the metaphorical equations, see section 4.2)[2].

1 The two systems can be both read at the individual or populational level, but the sense of the system changes depending on the level. Intuitively, we would prefer the individual level for ontogenesis, where g stands for an individual nucleic acid, and populational level for selection, where g stands for the population vector of genes. However, to compare the two systems requires to interpret them at the same level.

2 The metaphor of information processing in biology (*i.e.* populations of genes are informed by natural selection, and individual genes express this information throughout ontogenesis, *e.g.* OLF 2003:174) comes, in our view, from the supposed forcings described by our two systems of equations: what forces,

Frequency dependence is a particular case of selection where $E=g$. Thus for frequency-dependence, we get:

$$E_{t+\Delta t}=s(g_t) \qquad (2)$$

Comparing (1) and (2) helps to distinguish between "selective construction" (that is, a modification of the selective environment through the selective process itself, without any entanglement with ontogenesis: equation 2) and "ontogenetic construction" (modification of the selective environment through the ontogenetic process: equation 1). We called the last niche construction here.

Glossary

Here we aim at specifying in which idiosyncratic sense we (and sometimes authors cited here) take some of the words discussed in the main text (the corresponding sections where the concepts are discussed are given).

Adaptation: in this chapter, adaptation means fit (section 4.1).

Classical selectionist scheme: the selectionist scheme where ontogenesis as a dynamical process is neglected (sections 2.1 & 2.6).

Entanglement: non separability of scales[1].

Environment: "the surrounginds of a given organism or population, including all the contents of this regions" (Godfrey-Smith 1998:152). Here Godfrey-Smith reduces Brandon's three concepts of environment into one (see selective environment below).

Gene: active, faithfully replicating, piece of nucleic acid (section 2.2).

Genotype: class to which a gene belongs (given its sequence or its reaction norm)[2].

Genotype-phenotype map: see norm of reaction (section 2.3).

Fit: adaptedness (to given constraints) (section 4.1).

Fitness: adaptedness or expected geometrical rate of increase on a given time-scale (including rate of non-decrease by mere survival) given adaptedness on this time-scale[3] (section 2.4).

Forcing: any structure imposed onto a system, or, in particular, onto the dynamics of a variable. Forcing entails the absence of retroaction[4].

Invariant : figure that is symmetric with respect to a specified set of transformations. In this paper, the transformations are mostly translations in time. The invariant here is a set of dynamical equations, including the set of constant parameters (section 1.1).[5]

informs.

1 Our use of this term departs from its strict meaning in quantum mechanics.

2 We draw the reader's attention to the fact that this definition departs from the usual definition, where a genotype stands for a class to which an gene or organism belongs based upon "the postulated state of its internal hereditary factors, the genes" (Lewontin 1992).

3 Here we use the so-called propensity concept. The time-scale criterion is meant to subsume, as far as possible with so few words, both concepts of "long term fitness" (Thoday 1953) and of "expected time to extinction" (Cooper 1984), while remaining neutral as for the relevant time-scale (for instance, one might be interested in transient events).

4 Here we do not limit forcing to the temporal structures, in contrast with traditionnal meaning of the word in the field of classical mechanics.

5 Our use of this concept here is rather liberal. For an in-depth discussion of symmetry and invariance, see

Natural selection: the process described by the selectionist scheme (section 2.1)[1].

Niche (OLF's sense)**:** "the sum of all the natural selection pressures to which the population is exposed. A population *O's* niche is specified at time *t* by a "niche function" $N(t)$ where $N(t)=h(O,E)$. O is the population of organisms, and E is O's environment, both specified at time t. The temporal dynamics of $N(t)$, equivalent to niche evolution, are driven by both O's niche-constructing acts, and selection from sources in E that have previously been modified by O's niche-constructing acts, as well as by the dynamics of E that are independent of O's niche construction." (OLF 2003:419). Note that this definition departs from those used in ecology (this thesis, chap.1).

Niche construction (OLF's sense)**:** "the process whereby organisms, through their metabolism, their activities, and their choices, modify their own and/or each other's niches. Niche construction may restul in changes in one or more natural selection pressures in the external environment of populations. Niche-constructing organisms may alter the natural selection pressures of their own population, of other populations, or of both." (OLF 2003:419).

Niche construction (our sense): ontogenesis which is not separable from selection.

Norm of reaction : "the function that maps the space of environmental sequences into the space of phenotypic outcomes for a given genotype. (…) Of course, in practice, these are specified as the mapping of partial environment (e.g., temperature) into partial phenotype (e.g., body weight) for a partial genotype." (Lewontin 1992:141, the concept is due to Wolterreck 1909:135, see Sarkar 2006:80).

Ontogenesis: the process whereby a gene (or any other replicator) modifies its environment.

Phenotype: effect of a gene on the world. The phenotype of x is that part E_x of the environment E for which $P(E_x / x \;\&\; y) = P(E_x / x) \neq P(E_x / y)$, where y stands for any other genotypic entity in the system[2].

Phenotype-fitness map: selective invariant. As the reaction norm, the selective invariant includes environmental dimensions (section 2.3).

Replication (broad sense): growth and persistence, multiplication and survival

Selection: the process whereby an environment modifies a gene's fitness.

Selection (or selective) pressure: short term selective invariant: selection coefficients or selection gradients (*i.e.* differences in fitness[3]), or long term selective invariant: *e.g.* pay-off matrix (section 3.6).

Selective environment: the environment "measured in terms of the relative actualized fitnesses of different genotypes across time or space" (Brandon 1992). Brandon defines the

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Brading & Castellani (2008).

1 As Hodge (1992) remarked, Darwin did not explicitly define this term. For conceptual accounts see *e.g.* Endler (1986:4 gives a similar definition, 1992), Brandon (2008).

2 We draw the reader's attention to the fact that this definition departs from the usual definition, where a phenotype is a class to which an organism belongs based upon "the observable physical qualities of the organism, including its morphology, physiology, and behavior at all levels of description" (Lewontin 1992).

3 Endler (1986:xii) lists at least two meanings of selection gradient: (1) geographic gradient in natural selection (2) the rate of change of fitness with trait value (Lande & Arnold 1983). Here we use the second sense.

selective environment in contrast with the external environment (“the sum of total of factors, both biotic and abiotic, external to the organisms of interest”) and the ecological environment (“those features of the external environment that affect the organisms' contributions to population growth”). (It should be noticed that OLF do not cite Brandon, thus we cannot conclude that their use of the word conforms to the definition given here.)

State: set of variables, at a given point on the dimension of reference. In our case, the reference dimension is time (section 1.1).

Time scale: characteristic time of a process (*e.g.* mean lifetime or half-life time).

Time scale separation: the theoretical procedure whereby, when dealing with a particular dynamical process, one ignores other possibly relevant processes because they are either fast enough or slow enough. When two dynamical processes are time separated, their dynamics are invariant with regards to each other.

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