Assessing the Prospects for a Return of Organisms in Evolutionary Biology

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ABSTRACT – An argument has been raised from various perspectives against the Modern Synthesis (MS) in the past two decades: it has forgotten organisms. Niche construction theorists (Odling-Smee et al., 2003), developmental biologists like West-Eberhard (2003) and Evo-Devo elaborated various views which concur on a rehabilitation of the explanatory role of organisms, formerly neglected by an evolutionary science mostly centered on genes. This paper aims at assessing such criticisms by unraveling the specific arguments they use and evaluating how empirical findings may support them. In the first section, I review the usual critiques about the way MS treats organisms and show that the organisms-concerned critique is multifaceted, and I use the controversy about units of selection in order to show that purely conceptual and empirical arguments have been mixed up when organisms were concerned. In the second section, I consider successively the challenges raised to evolutionary MS by structuralist biologists and then the developmentalist challenge mostly raised by Evo-Devo. I distinguish what is purely conceptual among those criticisms and what mostly relies on recent empirical findings about genome activation, inheritance, and epigenetics. The last section discusses another program in MS, namely “evolutionary transitions” research, as enquiry into the emergence of organisms.

KEYWORDS – Organism, Modern Synthesis, structuralism, Evo-Devo, genotype-phenotype map, evolutionary transitions, externalism, explanation

Introduction

For at least two decades, the Modern Synthesis as a framework for evolutionary biology in general has been challenged in many ways. In several cases, the status of organisms in this vision of evolutionary biology was at stake (e.g. Bateson 2009). Recent attempts to produce either an extended evolutionary theory, or a novel kind of synthesis (Pigliucci 2009; Gould 2002; Gilbert, Opitz, and Raff 1996; Gilbert and Epel 2008; Odling-Smee, Laland, and Feldman 2003), indeed converge on the idea that “organism” was the neglected concept in evolutionary theory and
that extending such a theory would provide an accurate understanding of this crucial phenomenon, as well as renew our general idea of evolution by putting organisms back in the center of the stage.

This highlighting of organisms is striking because the organism provided, since the second half of the eighteenth century, the main scheme by which the life sciences captured their object. While many authors from the past centuries, including anatomists and physiologists in Galenic or Aristotelian frameworks, considered living entities as bodies animated by a soul, the advances in physiology like Bichat's or Haller's, in embryology like Wolff’s *Theoria Generationis* (1758) and later Von Baer’s *Entwicklungsgechichte des Thieres* (1828), concurred in thinking that the proper object of life sciences should be a set of parts organizing itself as a whole, the development and the functioning of this specific kind of entity being the proper field of, respectively, physiology and embryology (Rittersbuch 1964; Barsanti 1994; Huneman 2008). Even if scholars disagree on how this process occurred, when exactly and why, the shifting regime in the general scheme and object of life sciences at this time, and the crucial role of “organismality” is not contested.

Interestingly, in his *Critique of Judgment* (1790) Kant captured in a concept many aspects of this general idea or scheme of organisms. He spoke of “natural purposes” and claimed that organisms were self-organising entities that would fall under such a concept, thus requiring a unique kind of intelligibility.1 The details of his analysis are not relevant here, but it is the case that Kantian conceptions were intertwined with the anatomy and embryology of Von Baer, Cuvier, Geoffroy Saint Hilaire, Goethe etc. (Huneman 2006; Richards 2002; Sloan 2003; 2007). All this historical configuration of theories and evidences led to a transcendental morphology relying on Geoffroy’s *Philosophie zoologique*, a school of thought which forged the concept of *Bauplan* (Rehbock 1983; Sloan 2003; Balan 1979), later borrowed by Gould and Lewontin to designate the specificity of organisms as that which was omitted by the hardened (Gould 1983) Modern Synthesis triumphant in the 70s.

The main question of this paper is, more precisely, the nature of the challenges raised by various alternatives to the Modern Synthesis (MS) when it comes to the status of organisms. I claim that there are indeed several projects and issues not to be confused, implicitly enveloped in the same critique concerning the neglect of organisms. Considering both the structuralist and the developmentalist attacks on MS, which can be seen as two readings of the idea of *Bauplan* in Gould and Lewontin

1 “It is then—and for this sole reason—that such a product, as organized and organizing itself, can be called a natural purpose” (Kant 1790/1987, §65, V, 410).
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(1979 – hereafter GL), I show that some issues are empirical and others conceptual, and that in some cases the MS is not guilty of the faults it is supposed to have made and, in other cases, it is able to deal with the issues. I will then explore another aspect of organisms that evolutionary theory MS-style approached recently, which is the so-called “evolutionary transitions” program. In this context, whereas some authors claim that MS has forgotten the basis of its biological thinking, namely organisms, actually MS may have resources to investigate it.

**Darwinism and the Modern Synthesis on Organisms**

There is no doubt that organism was a central concept in Darwin’s formulation of evolutionary theory. Darwin saw evolution as the transformation of the forms of organisms and this explanandum had to be explained by a natural selection that was targeting organisms (Ariew 2008). The shift towards what Denis Walsh (2010) calls “suborganismal biology” occurred with the Modern Synthesis. As Sarkar and Gilbert put it, this turn pervaded the whole of biology.

The original goal of evolutionary biology was the reconstruction of life’s phylogenies – how fish became amphibians, how invertebrates became vertebrates, etc. (Bowler 1995). By the mid-twentieth century, this was transformed into a science that studied the differential assortment of genes in each generation. “The study of mechanisms of evolution falls within the province of population genetics” (Dobzhansky 1951). Developmental biology became the study of differential gene expression rather than the attempt to identify the rules underlying morphologic form (see Gilbert, 1996; Gilbert et al., 1996). Similarly, animal behavior gave way to sociobiology and behavioral genetics, and all branches of physiology and anatomy were put on a gene-oriented base. (Gilbert and Sarkar 2000, 2)

Immediately prior to Darwin, we had a comparative anatomy in a Cuvierian manner, which emphasized biological functions as the ways organisms would cope with their environment in order to be viable (see Ospovat 1978). There was a morphology in the style inaugurated by Geoffroy Saint-Hilaire, which argued that bodyplans were invariant among large groups of organisms, and that such structures had to be investigated across all phyla. Yet both of them shared the same explanatory focus on traits and features of organisms. They also relied on explanatory principles deeply rooted in the very concept of an organism, namely the “principle of the conditions for existence” for Cuvier and comparative anatomists, and the “principle of connections” for Geoffroy. So at the
level of those very deep epistemological structures Darwin’s project was not an absolute break, as Ospovat made clear by emphasizing the role of morphologists in the founding of Darwin’s theory (see also Sloan 2003).

The eclipse of organisms in MS and the variety of critiques

When people consider evolution as the change of gene frequencies in populations, as in many evolution textbooks, clearly the level where explanation had to be sought somehow bracketed organisms, since the relevant entities were only genes and populations. However, the authors of the Modern Synthesis disagreed on the role of organisms in this general setting. Granted, population genetics has shown that natural selection was a process likely to drive significant evolutionary changes with no need of macromutations if one assumes a Mendelian non-blending inheritance (Gayon 1998). This achievement of Fisher, Wright, and Haldane therefore triggered the evolutionary synthesis by elaborating the theoretical framework within which the process of natural selection was understood (Mayr and Provine 1980). However, not all authors of the Synthesis, e.g. Simpson, Mayr, Dobzhansky, Fisher or Huxley, agreed on the meaning of the concepts from population genetics. For instance, Mayr objected to the standard definition of evolution in terms of changing allele frequencies, preferring a definition in terms of properties related to organisms. “Evolution is not a change in gene frequencies, as is claimed so often, but the maintenance (or improvement) of adaptedness and the origin of diversity. Changes in gene frequency are a result of such evolution, not its cause” (Mayr 1997, 2093).

Nevertheless, even if there was no massive agreement on this definition of evolution and the consequences for the status of organisms, one can still easily see that the central character of population genetics as the science of the process of evolution would still raise the issue of the non-centrality of organisms. Granted, Ernst Mayr (1959) famously criticized “beanbag genetics,” namely the view that evolutionary biology could treat real populations like the simplest models of population genetics, as sets of genotypes on which genes are like beads on a necklace. Yet, even if one endorses this critique that the population-genetics-centered Modern Synthesis misunderstood genotypes, it does not settle the question of organisms in such a theory. Population genetics indeed tracks the fate of alleles according to their fitness values, properties of environments and some conditions about their relationships (e.g., epistasis, dominance, etc.) but the fact that those alleles constitute a genotype of an organism is

\[2\] In the same sense, Dobzhansky wrote: “Talking about traits as though they were independent entities is responsible for much confusion in biological and especially in evolutionary thought” (1970, 65).
not as such relevant. Therefore if the knowledge of the processes of natural selection and drift is provided mostly by population genetics and if those are the processes explaining evolution, adaptation and diversity, it is plausible that organisms as such are not relevant as *explanans* in a science of evolution. Analyses like Depew (2010) distinguish two branches in the Modern Synthesis, an Oxonian one – Fisher, Haldane, and Ford – which ultimately led to adaptationism and the gene’s eye view, and an American one, represented by Dobzhansky, Simpson, Mayr, which in the 70s was eclipsed by adaptationism. Historically speaking, the eclipse of organisms is more akin to the first branch, and the vindication of organisms is supported by the second one.

Yet the critique raised against a population-genetics-centered understanding of the Synthesis may be very different according to what exactly is criticized. People could claim against MS as centered on population genetics that, first, organisms are not explained by such a theoretical approach, because a theory in which at some point it could be possible that there are no organisms, cannot explain how organisms are, why they transform, etc.\(^3\) Especially, it means that such a theory cannot really understand the big changes in patterns of organisms, and here the critique concurs with the refusal of assimilating microevolution (understood through population genetics) to macroevolution (which appears for example in phylogenetics), as was clearly formulated by Simpson (1953).\(^4\) The critique of atomization in GL is a good example: adaptationists are not able to understand organisms as an integrated set of traits because they explain the traits one by one (as adaptations) and therefore cannot understand why it is the case that they are together in such a coherent whole.\(^5\) GL explicitly reject a conception present at the beginning of the Modern Synthesis, for example with Huxley, who said, “every organism cannot be other than a *bundle of adaptations*” (1942, 420).

Second, the critique can mean that organisms should be part of the *explanans* of evolution, so that there is something incomplete in a view of evolution centered on the dynamics of genes in populations. In this vein, Pepper and Heron (2008) argued that the concept of organism has an explanatory role to play in evolutionary biology, especially for comparative purposes, even if several domains would allow for different

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\(^3\) For ex. Burian describes the critique of genetics in this way: “the disagreements were based in part on the absolute inability of geneticists to show how genes could account for the *Bauplan* of an organism” (Burian 2005, 220).

\(^4\) See Gould (1994) for an account of Simpson’s change of view on this issue between 1944 and 1953.

\(^5\) “Organisms are integrated entities, not collections of discrete objects. Evolutionists have often been led astray by inappropriate atomization, as D’Arcy Thompson (1942) loved to point out” (Gould and Lewontin 1979, 585).
concepts. More precisely, this second critique – targeting the explanatory of MS, not the explananda – can be subdivided. That is, one could argue that an explanans is missing in the theory, for example that the development of organisms provides a view of variation that is different from assimilating variation to mutation or recombination, which are the only cases handled by population genetics (Amundson 2005; Gilbert 2003; Kirschner and Gerhardt 2005; Burian 2005; Gould 1977).

A good recent example is Odling-Smee, Laland and Feldman’s work on niche construction, entitled “the neglected process in evolution.” They claim that whereas natural selection in population genetics explains a part of evolution, yet the change brought upon environments by organisms themselves, is neglected in the usual ways of modeling evolution by considering selective pressures independently of what organisms do. Or, one could also argue that the MS explanations in fact should presuppose the organism. For example one could say that the constraints, which are recognized in optimization models in behavioral ecology or population genetics, are actually expressing the fact that genes are genes of an organism, so that not any combination is possible because the integrity of the organism constrains the possible combinations. The critique developed by Walsh (2003) according to which MS cannot explain adaptation but only its spreading and that one has to resort to intrinsic properties of organisms to understand the arising of adaptation, is clearly of the same nature. Under the first point, MS is explanatorily incomplete; in the second, its explanations lack radicality because they rest on hidden, organism-related, assumptions.

Yet, the explanatory insufficiency of MS regarding organisms can also be seen according to two axes. The first axis is the organism versus environment distinction. Here the critique is basically an anti-externalist one (sensu Godfrey-Smith 1996); i.e., critiques argue that selectionist explanation considers only a causal arrow going from environmental structure and changes to traits of organisms (via genotypes), the environment somehow shaping passive organisms. The niche-construction critique is obviously of this nature, as well as Bateson (2008) emphasizing, on the basis of studies of behavioral imprinting, that “decision-making and adaptability of the organism is recognized an important driver of evolution.” Now take West-Eberhard’s critique of MS based on the ideas of active phenotypic plasticity. She argues that evolutionary changes are

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6 Although the fact that variation is more general than point mutations was recognized already by Dobzhansky (1937, 170)

7 Arguing that MS captures a pseudo process of evolution, Walsh (2003) indicates that MS lacks radicality in its explanantia.
mostly driven by the fact that organisms of a given genotype create new phenotypic variants in the face of changing environments and that genetic change somehow follows from this first move. “I consider genes followers, not leaders, in adaptive evolution” (West-Eberhard 2005, 6547). Therefore organisms’ phenotypes have the lead in evolutionary dynamics, unlike the scheme suggested by population genetics. Here West-Eberhard’s critique also develops along another axis, the organism versus genes opposition. The thesis that invention of novel phenotypes leads evolution clearly contrasts with the roles alleles and genotypes receive in the classical MS explanation, within which they are primitive, in the sense that differences occurring in genotypes are at the principle of evolutionary explanations.

![Explananda Diagram]

Table 1. Summary: One can critique the role of organisms in MS at the level of:

However, all these kinds of critiques are still equivocal. One does not know whether along those five lines authors criticize the MS biologists because they did not know some facts that molecular biology, ecology, and other disciplines recently discovered, or because they did not have, and provide us, the concepts to capture the core phenomena of evolution and adaptation. In other words, I wonder which of these critiques are conceptual and which empirical. In order to ask this question I will
consider first a well-known topic: a controversy involving organisms in MS is the issue of units of selection, and yet, this controversy has often been misconstrued, so the next section, detailing how this controversy involved organisms, will allow us to make important distinctions regarding the debates.

*The units of selection as a test-case*

The classical MS picture raises various critiques concerning its explanatory insufficiency with regard to organisms. Yet in most of the writings of the MS, the organism in fact had a dual status: although it was bracketed in the explanatory structure that captured the working of natural selection (i.e. population genetics), it was often at the front of the stage when considering the target of selection.

However the debates about levels of selection initiated by Dawkins (1976), which included many arguments designed to prove that natural selection really deals with organisms and not genes, are in fact very intricate and include radically different kinds of problems. One often presents the controversy about gene selectionism as a conflict between selection on genes and selection on organisms. This rough presentation is actually very confusing when one wants to understand why such a critique of gene selectionism came about.

Gene selectionism is the position according to which the targets of natural selection are replicators—and the genes are indeed the replicators, not the organisms. Two independent arguments were mainly used. The first ones are cases of evolution of altruism, which after Hamilton's theory of kin selection (1963), compel theorists to consider selection at the level of genes and not organisms (because, there, altruism is an evolutionary contradiction). The second ones are the cases of outlaw genes like segregation distorters, which display natural selection occurring among genes, with no regard to organisms. Those two arguments are quite different, because the second one is a fact about some instances of selection, which does not entail something general about natural selection (it is a process of genic selection, but not a thesis of genic selectionism). In contrast, the first provides a model for some problems for evolutionary theory and such a model may entail a general view of selection but can also be held for itself, in the restricted area of social behaviors.

Actually there were two very different ways of objecting to gene selectionism, instantiating two different issues. The first one, which was Gould and Mayr's initial reactions,\(^8\) is that selection does not “see” al-

\(^8\) See arguments in Gould (1990) and Mayr (1997).
leles, but only organisms. This critique has been formulated more generally by Brandon (1988) in terms of “screening off.” Without the probabilistic formulation of screening off, the argument is that there cannot be a change in genotype that makes a difference regarding the outcome of selection without having a change in phenotypes, whereas changing the genotype will not necessarily change the outcome of selection (because it can lead to the same phenotype). So it is only phenotypes which necessarily make a difference (even if they result from change in genotype) in what is selected and not genotypes. This obviously attests that the gene selection vs. organism selection debate is here in fact a debate about genes (or genotypes) vs. phenotypes selection. Dawkins’s opponents are understood as concluding in favor of organism selection because the phenotype is more of an organism than its genes.

The second class of arguments is paradigmatically akin to the one formulated by Sober and Lewontin (1982). They argue that gene selectionism, though able to track the evolutionary changes (what they call “bookkeeping”) – which is not a surprise given that evolution is precisely defined in terms of changes in allelic frequencies – does not provide an access to the causal processes at stake. Their crucial example is the case of heterozygote superiority, like the sickle-cell anemia case. Famously, the recessive allele for this locus produces a form of anemia (by altering the molecules able to fixate oxygen) so that the recessive homozygotes are lethal; yet in some regions (esp. Africa) the heterozygotes display resistance to malaria, so that in the end their fitness is higher than the one of dominant homozygotes. In this case, what is causally relevant are the genotypic fitnesses, namely the fact that the heterozygous individuals are of higher fitness, which corresponds to the fact that there will be selection for malaria resistance. The outcomes of the selection process are given by computing the genotypic fitnesses and not the allelic fitnesses. Of course, one could always derive the allelic frequencies from the genotypic frequencies and, therefore, write the dynamics in allelic terms, but this clears up the causal and explanatory fact, namely the highest fitness of heterozygotes (because other genotypic frequencies could indeed lead to the same allelic frequencies). The critique concerns organisms because it is genotypes and not alleles which condition organisms’ phenotypes; but in the first place, it is really about selection targeting genotypes rather than alleles.

So the rough picture, organism selection vs. gene’s eye view, in reality uncovers two debates: “selection on genotypes vs. selection on phenotypes,” and “allelic vs. genotypic selection.” They may also be distinguished as (1) a question about the causal level where selection takes place—and then the screening-off argument would say it is the pheno-
typic level; and (2) a question about the smallest units whose change will make a difference in fitness values in a given environment (and here the heterozygote superiority argument shows it is the genotype of a locus—which is still at the genic level—and not the alleles). Brandon (1988) calls them the question of the level of selection, and the question of the units of selection.

Moreover, the status of the arguments used in those two cases is different, if one wonders up to which point those are empirical questions. The first issue, phenotypic vs. genetic selection, is somehow conceptual. In any world, the difference between phenotypes and genotypes is such that you cannot alter the fitness values by changing genotypes without changing the phenotypes. Therefore you get the screening-off argument. So this critique of genetic selectionism—which vindicates in many cases organisms as the level of selection—"is somehow conceptual.

On the other hand, the status of the heterozygous superiority argument is less clear. You can indeed imagine worlds where there is no epistasis and dominance, and finally no heterozygous superiority. In those worlds, the ordering of genotypic fitness will follow from the allelic fitnesses and be uniquely entailed by them. And in a world with no epistasis, changing some alleles will not affect the phenotypes of the others and therefore their fitness, so that the alleles are indeed the smallest units such that fitness is stable across the environments. To this extent, there are possible worlds (plausibly, not the actual one) where the allelic selectionism—as the idea that you can explain the dynamics of selection by tracking the dynamics of a given allele—is true. So deciding the allelic vs. genotypic selectionism issue is in the end an empirical question (see also Okasha 2006 on this point).

Interestingly, those two kinds of contestation of the gene’s eye view, which are two ways of reasserting the role of organisms in evolution (as phenotypes against genotypes, as holistic systems of traits against isolated alleles) without arguing for any extension of MS, may be distinguished as a conceptual vs. an empirical one. This is enough to show that the longstanding concern for an explanatory insufficiency of MS regarding organisms encompasses both empirical and conceptual issues. For example, take West-Eberhard’s view of evolution; it relies on empirical extended work on plasticity. “A very large body of evidence . . . shows that phenotypic novelty is largely reorganizational rather than a product of innovative genes.” Yet she needs also a rather conceptual reworking of the relationships between phenotypes and genotypes—namely, she

9 Except cases of genic selectionism, where the phenotypes are precisely the physical and chemical properties of the DNA sequence itself.
justifies the leading role of plastic phenotypes vs. genes in the following terms:

Any new input, whether it comes from the genome, like a mutation, or from the external environment, like a temperature change, a pathogen, or a parental opinion, has a developmental effect only if the preexisting phenotype is responsive to it. Without developmental plasticity, the bare genes and the impositions of the environment would have no effect and no importance for evolution. (West-Eberhard 2005, 6544)

So now I will turn to the genuine critiques of MS, in order to disentangle in the same way various kinds of organism-related issues that are often confused.

Structuralists, Developmentalists and the Bauplan of Organisms

I propose an examination of two challenges to the MS, a more structural one and a line of argument relying on the evolutionary theory of development (Evo-Devo). Amundson (2005) developed a critical history of the non-MS view of evolution, in order to assess the challenges of Evo-Devo, and he connected the developmentalist challenge to the older structuralist view of evolution and biology in general. Here I distinguish the two trends, because it will appear that they do not exactly concern organisms in the same way in regards to evolutionary theory.

Bauplan, Kant and the General Organismic Challenge to MS

I tackle the question through the paper by Gould and Lewontin (1979) and the reference made to the idea of a Bauplan. Interestingly, on the one hand this term gestures towards the older transcendental morphology, which was essentially a quest for common structures of organisms across many lineages (Rehbock 1983), as exemplified by the reconstruction of vertebrate archetype by Owen (Owen 1992; 2007). Of course, GL does not criticize MS as such, but as a specific method called ‘adaptationism,’10 which atomizes organisms into separate traits and explains each of them as a result of natural selection, i.e., adaptation. So I will first consider GL’s idea of the Bauplan and wonder up to which point it is right to say that neglecting the Bauplan causes adaptationism – taken as a crucial trend in the MS (provided the historical caveats

10 There is a substantial literature on what “adaptationist” should mean, a question prior to the assessment of its validity, although GL did not exactly made the idea precise; see especially Sober 1996, Godfrey-Smith 1996, Lewens 2009.
stated above) – to leave organisms out of their evolutionary understanding. To this end, I will appeal to the Kantian concept of organism, which through the tradition of *Bauplan* studies is implicitly invoked by GL. Authors who used the idea, such as Meckel, Serres, Agassiz (1850) and Owen, were directly related to the idea of organism Kant elaborated and to some extent shared with embryologists like Blumenbach and later Von Baer. The *Bauplan* translates into morphology the idea of type as reached by the *Bildungstrieb* (Blumenbach) through the developmental process. Then I will consider the developmentalist and the structuralist challenges to MS as two conceptions realizing the alternative view of evolution advocated by GL.

The concept of *Bauplan* in transcendental morphology directly traces back to Kant’s view of organisms as integrated wholes that self-organise (Kant 1987, §65). Basically Kant, in building his concept of organism, is saying that organisms fulfill two criteria regarding the parts-whole relations they include, which make them “natural purposes.” First, they are such that the parts are what they are in virtue of the whole; second – in order to distinguish between technical artifacts which fulfill the previous criterion, and natural purposes as organisms – the parts are reciprocally causes and effects of themselves. This means that they are producing themselves according to the whole, in an epigenetic process which realizes a kind of blueprint. Kant says “produces” about this causal tie between parts, which means that their causal role towards another is not only formal – namely, a part conditions the form of another – but of real production. Therefore I take it as a view of organisms as essentially displaying ontogenetic processes.

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11 See Sloan 2003; Rehbock 1983.
12 For a historical account of this connection see Richards 2002; Sloan 2003; Reill 2005. There is a controversy about the extent to which transcendental morphologists after Geoffroy, or even embryologist contemporaries of Kant like Blumenbach, were actually Kantian (e.g. Richards 2001, vs. Lenoir 1989; Zammito 1992, etc.) but all this scholarly work shows that Kant’s philosophical conception of organisms captured something basic for the inquiries in morphology and embryology, even if it belonged to another metaphysical project.
13 So Kant writes: “Thus, concerning a body that has to be judged as a natural purpose in itself and according to its internal possibility, it is required that the parts of it produce themselves [hervorbringen] together, one from the other, in their form as much as in their binding, reciprocally, and from this causation on, produce a whole. . . . In such a product of nature each part, at the same time as it exists throughout all the others, is thought as existing with respect to [um…willen] the other parts and the whole, namely as instrument (organ). That is nevertheless not enough (because it could be merely an instrument of art, and represented as possible only as a purpose in general); the part is thought of as an organ producing the other parts (and consequently each part as producing the others reciprocally)” (Kant 1987, §65, 374).
14 This teleology differs from “mechanism” as the usual explanation of wholes from the parts (McLaughlin 1990). Kant has a specific notion of this “blueprint” that he calls “generic preformationism”, see Sloan 2002.
For the scientist, this means that organisms occur at two levels. First, given that the second criterion entails a specific causation between parts for which we have no analogue, the biologist must assume that there is an organismal pattern according to which organisms develop and function. This is a regulative presupposition, as Kant says (§75), meaning that without such assumptions one could not even investigate living things qua living. When he presents his theory of natural purposes, he writes,

if the thing must be possible only as a natural purpose, and without the causality of a rational being external to it, then it must be the case, that (. . .) the parts of this thing are bound together in the unity of a whole, and that they are reciprocally, one to another, causes and effects of their forms. It is only in this way that it is possible that, in the reverse way (reciprocally), the idea of the whole determines the form and the binding of all the parts: not as a cause, since it would be a product of art – but as a principle of knowledge [Erkenntnisgrund] of the systematic unity of the binding of all the manifold contained in the given matter for the one who has to judge. (Kant 1987, §65)

I emphasize that the teleological causation at work here, which makes sense of the first criterion – the whole as a cause of parts – is an ideal one, meaning that the “idea of a whole” is this compelling “principle of knowledge” at the principle of our understanding of organismal organization and development.

Then, at a second stage, such a presupposition of organismality can be cashed out in various regulative principles; for instance Cuvier’s principles of conditions for existence or Geoffroy’s principle of connections, according to whether one understands purposiveness as functionality, or as conservation of form (Huneman 2006). Then on the basis of those principles the scientist may reconstruct a pattern of organization as the aim of her study. So organisms occur first at the beginning of the enquiry, as this assumption which regulates the very investigation itself (under the form of regulative principles) and second, in the end, as the reconstructed patterns. Then, many organisms may share a pattern or, more precisely, the biologist can infer from many patterns a more general and abstract pattern common to, e.g., all fish or even all vertebrates. This is

15 “Strictly speaking, therefore, the organization of nature has nothing analogous to any causality known to us” (§65, 375). We are only acquainted to parts acting on parts, or wholes acting on parts via human craft and skills. The self-organization according to a regulative idea is just out of reach of our finite understanding, for Kant.

16 In the context of embryology, Kant talks of ‘original organization,’ a concept which met an important fate in the embryological writings of Pander, Kielmeyer, and Von Baer – see Lenoir 1984; Zammito 1992, 214-227; Huneman 2008, 314-324.

17 For example, in Cuvier’s paleontology it will be the shape of a dinosaur reconstructed according to the principle of conditions of existence, and its correlative principle of correlations – Discours sur
what in the tradition of Kant and especially Blumenbach and Von Baer, German morphologists as well as Owen would name Bauplan (Rehbock 1983; Ospovat 1980; Balan 1979; Schmitt 2001). As such, at each level - i.e. Geist, as an assumption and then as an objective of the enquiry - the Bauplan defines a set of constraints upon all parts of an organism.

Why therefore is the Bauplan a concept used against some fundamental tenets of the MS? To be sure, adaptationism ignores the holistic patterns of organisms because it just considers traits in their own rights. If we consider a frequent answer to GL's critiques, we can make sense of the difference here. Many evolutionary biologists (e.g. Mayr 1983; Maynard-Smith 1978) replied, in effect, that they recognize how the fact that traits are embedded in an organism places constraints upon those traits, and such constraints are therefore acknowledged within the models in the form of the trade-offs between various traits. GL think that trade-offs are not a sufficient way of understanding the constraints. The radical divergence however lies within the explanatory structure involved. Granted, MS biologists will acknowledge the holistic character of organisms by treating the constraints as trade-offs between traits – X cannot optimize in the same time its respiratory capacities and its metabolism rate, so there is a trade-off which selection will optimize, sometimes in virtue of a general tradeoff between components of fitness (survival / reproduction), and whose value will depend upon the environment. In this sense, the pattern of organism appears in the end of the study, as an explanation of why optimization fails, the suboptimality being still a signature of selection. However, in the Kantian-morphologist stance, organisms are involved at two stages – not only in the end of the investigation, where one has to finesse her hypotheses, but in the beginning when hypotheses are formed. Because of this epistemological discrepancy, recognizing constraints in the form of trade-offs fine-tuned by environmental demands will not allow MS models to account for organisms as such.

**The Structuralist Stance**

Structuralism is what GL call the “strong” Bauplan alternative to adaptationism. A Bauplan is a general structure upon which each species

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18 Although, as shown by Amundson in his edition of Owen (1849), Owen elaborated a version of transcendantal morphology closer to the British empiricists’ ideas of science.

19 "The notion of ‘trade-off’ is introduced, and organisms are interpreted as best compromises among competing demands. Thus interaction among parts is retained completely within the adaptationist program. Any suboptimality of a part is explained as its contribution to the best possible design for the whole. The notion that suboptimality might represent anything other than the immediate work of natural selection is usually not entertained" (Gould and Lewontin 1979, 586).
instantiates a particular variation. Here, the argument is that the forms of organisms as well as the main generalizations under which sets of forms can be ranged are not likely to be understood through an evolutionary approach based on a computation of varying gene frequencies. In essence, the objection against MS boils down to the fact that evolutionary dynamics in population cannot unravel commonalities of structure and shape that range across many phyla, evolved in very various environmental conditions. The point is much against externalism and it implies that in those theories, *explanantia* other than natural selection (sometimes self-organization, e.g. Kaufmann 1993; Depew and Weber 1996) are sought which does not tie organisms to their environments and, therefore, plausibly account for the extended commonalities we see amongst very different kinds of organismic life.

This is a neat challenge to externalism. Such a challenge received answers along the lines of MS, basically in the terms that Darwin once stated in the *Origin* (chap. 6). Namely, those common features are still resulting from one single ancestor, who emerged through natural selection in a given environment – and then stabilizing selection would account for the continuous existence of the feature. This discussion is also mostly conceptual, because no matter what natural selection empirically accounts for, there would be a structuralist argument available about the limits of natural selection (focusing on what transcends sets of various populations) and a reply along the abovementioned lines.

But, notwithstanding the value of those answers, such a position does not really challenge the role of organisms in classical evolutionary theory. Basically speaking, the explanandum is mostly shifted. It is not features of given organisms, but *commonalities of forms across many phyla* (or in other words the clustering of morphospace) that require explanations. So one can still argue that even if this project means giving up on externalism, it remains first, that genes may be able to account for many of those commonalities, if one considers developmental genes and second, that the other project of explaining *traits of organisms in populations* (and

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20 GL clearly reject structuralism in this sense. “We believe that English biologists have been right in rejecting this strong form as close to an appeal to mysticism” (Gould and Lewontin 1979, 593).

21 In the last section of the chapter 6 (“Difficulties of the theory”) of the *Origin*, Darwin contrasts the two highest biological laws – Cuvier’s conditions of existence and Geoffroy’s unity of type. He reduces the first to natural selection, and the second to unity of descent. And then he eventually reduces the latter to the former. Those characters that are identical through their differences between clades – i.e., homologies – are therefore due to natural selection at first stake, because it accounts for the plesiomorphic state of the character. The same kind of answer to structuralist /developmentalist attacks on selectionism is developed by Reeve and Sherman (1993), and many other defendants of MS.

22 Carroll (2005) advocates such a solution.
then, via trade-offs, organisms) is still likely to be carried on in the MS framework without reinforcing the explanatory role of organisms.

The Developmentalist Stance

Concerning its explananda, and its relation to MS, developmentalism is very close to structuralism. It embodies the weaker sense of Bauplan advocated by GL (Gould and Lewontin 1979, 595). Development does not immediately matter to MS because it is not relevant in population genetics, which only considers the phenotype-genotype connection as it exclusively matters to the replicative chances of alleles. Hence, anyone who contests such neglect of development makes a case for integrating the developing entities or organisms, within evolutionary theory, and against some of the main explanatory assumptions of MS. In the developmentalist challenge, often instantiated by the many branches of Evo-Devo, the GL notion of Bauplan should mean a set of developmental pathways. Some are very common across different clades, because precisely the early stages are shared by all lineages having common ancestors (Shank and Wimsatt 1986; Arthur 2000; Raff 1996; Kirschnner and Gerhardt 2005). An abstract sequence of developmental pathways therefore may explain the production of some organic entity common to many phyla, such as the tetrapod limb. This object is by definition not amongst the explananda of population genetics because it is common to many populations of many species in many environments. It calls for another kind of explanation than the drift-selection applied to alleles. The developmental Bauplan pertains to a higher generality than many traits proper to species which it yields and, therefore, rests on explanatory processes which may be more universal than the always environmentally situated selectionist explanation. “[T]o developmental biologists, there is a mechanistic universality in developmental processes despite any diversity of ultimate outcome” (Raff 1996, 22). Granted, developmentalism resembles structuralism about some explananda here (namely, commonalities), however it involves the developmental activity of organism amongst the explanatory factors, whereas structuralism opposes an ideal structure with its very general mechanistic underpinnings (see D’Arcy Thompson 1966). Developmentalists oppose the externalism proper to

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23 The distinction of inheritance (transmission of discrete traits in populations across several generations) and development (ontogenetic process of the individual form) is a cardinal assumption of population genetics and beyond, the Modern Synthesis. It was first stated by Morgan. See Amundson (2005), for comments.

24 On organisms as developing entities, see Nuño de la Rosa (2010).


26 On the idea of “developmental type” (instantiated by this example) see Amundson (2005).
MS because the explanandum of Evo-Devo are common developmental structures across clades (e.g., the vertebrate limb) and so cannot be understood relative to an environment through natural selection. The specific limbs variously instantiating the “tetrapod limb” have indeed been facing very varied environments.

In this sense of Bauplan, the concept of constraint is therefore understood in terms of developmental constraints, meaning that all the variations are not possible because in order to be efficient, the developmental processes preclude many of those variations and inversely make some variations more likely. There is more to variation than mutation and recombination (which happen at the level of alleles), which are the only sources of variation for MS: developmental rearrangements, such as the heterochronies (Gould 1977), or developmental variations in the outputs of cellular “core processes” (Kirschner and Gerhardt 2005), provide the set of possible large variations (often larger than point mutations and recombinations) which will be crucial in evolution (especially large scale evolution, where innovations occur). The constraints are not what make some trait unlikely to reach an optimal value because some other traits are already here, but those constraints are already presupposed in the forming of each trait, because they bear on the variations from which it will be made. So the rephrasing of developmental constraints in terms of trade-offs is less plausible when the Bauplan is understood in a developmentalist context than in a purely structuralist context.

But developmentalism means that basically, understanding development itself is necessary to understand evolution. Correlatively, evolution means now the “change of developmental pathways across time” (Carroll 2005). Therefore development is also included in the very explanandum of evolutionary theory, and this shift in the definition of evolution means that MS, based on gene frequencies, is not the adequate theory of evolution. As to the critique of MS alleged gene-centrism, there are of course many lines of research in Evo-Devo and critiques of MS have been formulated from many standpoints but its case for organisms in evolution could be very abstractly grounded on the following points. Recent findings of molecular biology demonstrated that the genes are

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27 Amundson (1994) distinguishes in this sense selection and constraints, as explanation bearing on the one hand on which variations are retained (i.e., the set of actual variations to be met), on the other hand on which variations are possible (i.e., the set of possible variations). This entails that constraints touch upon another explanandum than selection.

28 GL establish that developmental constraint is the main explanatory concept in the weak version of Bauplan biology: “(We do) not deny that change, when it occurs, may be mediated by natural selection, but (we) hold that constraints restrict possible paths and modes of change so strongly that the constraints themselves become much the most interesting aspect of evolution.” (Gould and Lewontin 1979, 596, my emphasis).
only activated through very complex systems that involve the whole cell, its surroundings, and often the whole developing organism\textsuperscript{29} (for some insights see Burian 2005; Sarkar and Gilbert 2000; Arthur 2000; Raff 1996). So organisms – at least during their shaping – play an active role in the specification of genes and cannot be seen only as the product of genes. To this extent, an evolutionary biology tracking the fate of alleles is not able to understand this circular process through which organisms are actively involved in their shaping process and, moreover, cannot reach a comprehensive view of evolution because it already presupposes developing organisms in the background of those alleles. Thereby the main critique here is (regarding our table 1) the lack of explanatory radicality. So whereas structuralism mainly states that MS could not understand \textit{Baupläne} as common structures across phyla, developmentalism also insists on the fact that the whole set of basic concepts used by MS – genes, genotypes, phenotypes – implicitly presuppose some assumptions about organisms (through the processes of gene activation).

Clearly, such a developmentalist viewpoint comes with an emphasis on organisms as self-organizing entities, in the sense of the second Kantian criterion of organisms. This criterion says that those entities are such that their parts are causes and effects of one another according to some idea of the whole. Development is just such a causal process which at the same time matches some idea of the whole organism: since the cells differentiate in a non-arbitrary way, involving discriminate gene expression according to epigenetic factors (even if we don’t know through which exact mechanism), then they develop according to an idea that we must assume at the basis of the process. Without assuming such an idea of the whole we could not distinguish between pathological and normal developments. And precisely, the developmentalist emphasis on epigeneticity, against the view that each cell would develop a program, confers a modern meaning to the Kantian theory that the involvement of an idea of the whole – which would be provided by the DNA program – is not enough to capture what an organism is, but should be supplemented by the activity of parts in the shaping of the whole (here epigenetic regulations, “core processes” \textit{sensu} Kirschner and Gerhardt, which take place within the cell, etc.). The Kantian idea of organisms with its double criterion seems adequately to capture the meaning of organisms in the developmentalist stance.

Most generally, what is at stake in developmentalism as a challenge to MS is the development of organisms as a way through which genotypes and phenotypes are connected. Vindicating a role for development in evolution means that it is not enough to state that phenotypes result

\textsuperscript{29}As well as organism’s behaviour, see Bateson 2008, 33.
from genotypes, and therefore to consider phenotypes just as what biases the reproductive chances of genotypes. Yet – in the light of my previous examination of levels of selection – the question remains whether such challenge is a conceptual shift in evolutionary theory or concerns the empirical corroboration of evolutionary theory and therefore may be wrong. To get a better idea of this, consider the set of possible genotypes as a genotype space. To this genotype space (GS) corresponds a set of all possible phenotypes (PS).

Fig. 1 Phenotype-genotype Map

As we know, each phenotype may correspond to several genotypes, since several genes or sets of genes have the same phenotype (Fig. 1). And then, in between those two spaces, lies the space of possible developmental pathways (DS). Here again, each point in GS may correspond to several points in DS, and several points in DS may correspond to a same point in PS, namely, several developmental pathways may lead to the same phenotype. The idea of “canalization” put forth by Waddington, exactly expresses that several points in the GS reach the same point in DS. But, several points in DS may correspond to one genotype (plasticity) and also to one phenotype (canalization). So we have between those 3 spaces several possible many-to-one mappings.

In this context, the main assumption of the MS is that we can bracket the developmental space, namely, consider only the mappings between GS and PS – because whatever the developmental pathways going from a genotype (a point in GS) to a phenotype (a point in PS) does not make a difference to the evolutionary outcome. But this is not at all a con-
ceptual impossibility. In effect, there are specific configurations of the GS-DS and DS-PS mappings such that we are justified in neglecting what happens in DS. Indeed, the fact that several images of one point $g$ (from GS) exist in DS does not prevent us to treat the neighborhoods of point $g$ as having a single neighborhood image in PS and this means that what matters in evolution is only the application from GS to PS. Basically, no matter the many-to-one relationship between DS and PS, the topological relationships in GS are continuously transformed according to a given application in PS, so we do not need to consider DS because we can consider that a unique function projects GS into PS. (Fig. 2a) Of course, to decide this is clearly empirical. There is a set of possible triplets of intermapped spaces (GS-DS-PS) which is such that this condition is realized (Fig. 2a) and a set where it is not (Fig. 2b). Only experience tells us to which set the actual triplet GS-DS-PS belongs.

And moreover, it is clearly possible that, even if the actual triplet GS-DS-PS is such that one cannot in general neglect DS, in some vast regions of GS it is locally the case that the 3 spaces behave as if a single function can project GS into PS, so that in the end we can locally neglect DS. This may explain why the main assumption of population genetics, which neglects development (Gillespie 2004; Lewontin 1975; Amundson 2005), has been so powerful to explain evolution and adaptation in many cases. The reason is that those cases belong to such “well behaved” regions of GS.

Therefore, it could be the case that empirical findings now – because we consider other regions or more extended regions of the GS and the PS – entail the necessity also to consider the developmental space in order to understand the evolutionary dynamics. Such a move plausibly occurs when one considers more extended regions of the GS than the ones considered in usual population genetics models, for example when one deals with genes conserved in many clades, so in very wide regions of the GS, the larger a region, the higher the chances that it will not be “well behaved.” Once again, this question is an empirical issue and does not contradict the fact that the main assumptions of MS were thoroughly justified when it came to provide a conceptual framework to the empirical data that we had previously.

The developmentalist challenge is a revision of the status of organisms in evolutionary theory driven by the necessity to consider the way organisms develop in order to supplement, in large regions of the G-space, our understanding of evolutionary processes. This expansion of the regions of G-space means that such revision of MS occurs when one should consider macroevolution. The conceptual argument for this discontinuity is, once again, the fact that considering larger regions of P-space entails
higher chances to be obliged to consider the role of D-space in the mapping between G-space and D-space; but this conceptual argument is not enough, since only empirical findings can tell us something about the actual shape of those mappings.

Fig. 2 - A: Mapping such that considering D-space is not evolutionarily relevant; B: mapping where D-space is explanatorily relevant in evolution.

As such, the MS could in principle have the conceptual resources to take developing organisms into account in its explanatory apparatus, and indeed it did do so for a long time. What Evo-Devo, then, emphasizes is not the inability of MS to understand the fact of organisms, but the empirical necessity for a theory of evolution at a large scale to take into account how various organisms develop.

The Fact of Organisms Under Focus of Neo-Darwinian Evolutionary Theory

Until now, I interpreted Kant’s second criterion of organisms in terms of the epigenetic relationship between parts (see Zumbach 1984; Huneman 2007). Yet, the recent advances of evolutionary theory offer a way to understand this criterion in terms of evolution by natural selection. Summarizing various lines of research on multilevel selection and evolutions of levels of individuality (esp. Maynard-Smith and Szathmáry 1995; Michod 1999), Wilson and Wilson actually wrote, “Even genetic and developmental interactions within a single individual can be regarded as social, since the organisms of today are now known to be the social groups of past ages” (Wilson and Wilson 2007, 329).

This means that an organism is a set of parts characterized by specific causal relationships, but that such specificity calls for an evolutionary
understanding. The parts are somehow the descendants of previously autonomous living entities and the fact of organisms is basically the fact that at some point freely living cells entered into a process which yields multicellular life. Such a process is likely to be understood in evolutionary terms. So those biologists who are interested in explaining the biological fact of organisms as an historical result are saying that the kind of specific binding which ties the parts of organisms and which makes all of them somehow conditioned by all the others (i.e. Kant’s second criterion), results from evolutionary history, and can be explained in a neo-Darwinian manner. As Dawkins puts it, why do genes come packed into genotypes, and those “embedded” within organisms?

Many critiques of the role of organisms in MS indeed insisted on the fact that explanatory resources would implicitly rely on organisms while explicitly taking only genes and populations as explanantia. However, the “evolutionary transitions” project, asking in the first place how evolved are those individuals such as genes, cells, multicellular organisms, or societies – all of them able to be units of fitness – brings the very fact of organism under scrutiny. Kant thought that we have the concept of natural purpose, which is explicated into the two aforementioned criteria, and that organisms realize this concept. However, he was very clear on the fact that there could have been no organisms. In other words, natural purpose is an empirically conditioned concept, meaning that if there had not been organisms in the world, then we would not have had to forge the concept of natural purpose. Yet the novelty of the evolutionary transitions project, in this light, is that it aims at explaining such primitive fact, possibly along the lines of MS.

Precisely, the main explanatory scheme of the evolutionary transition project, as it is made clear by Michod (1999), is a multi-level selection process, through which basically selection on the low-level entities such as cells or genes, and selection on high-level entities such as organisms or chromosomes, compete in a way that makes selection on low-level entities subordinated to the selection on high level entities. This remains plainly in the field of MS because it does not require any other explanation than natural selection on variations.

The work by Michod and colleagues provides two kinds of overview of the evolutionary origins of multicellular organisms. The first kind (Michod 1999) is a general set of multi-level selection models that encom-

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30 “Now it is true that the concept of a thing as a natural purpose is empirically conditioned, i.e. a concept that is possible only under certain conditions given in experience; yet it is a concept that cannot be abstracted from experience but is possible only in terms of rational principle used in judging the object” (§74, 396).
passes all the main kinds of transitions. In each stage the main question is to understand what would repress competition among low level entities and will therefore provide a reason for maintaining the subordination of high level selection upon low level selection, given that by definition there is always a prime to defection (i.e., that low level entities which do not cooperate with others and increase their own reproductive levels at the expense of the collective carry a selective advantage). Another kind of explanation is more directly directed toward the explanation of multicellular organisms. Michod and colleagues took as a case study algae from the genus Volvocidae. Among this genus, interestingly some species are individuals made of single cells, some of very few cells, whereas in other species, Volvox carteri, they are of multicellular organisms. In this sense, understanding the reasons why this lineage turns to multicellularity provides an insight into the evolution of multicellular organisms. In the models (e.g. Michod et al. 2001; 2003), the key factor is the division of labor between cells, some of them specializing in reproduction (giving up flagella) whereas other specialize in motility and consumption. The model divides fitness into its two components, survival and reproduction, and each type of cell embodies one dimension of fitness. The shape of the fitness function (relating value of survival and value of fertility), namely its concavity, proper to each kind of possible species of algae, predicts whether finally the division will go to completion and makes the two types of cell coalesce into a single multicellular entity. Here, as compared to the general sketches of evolutionary transition described previously, the multilevel selection model interestingly has to break fitness into its components to explain the division of labour necessary for the occurrence of multicellularity. The model explains the fact that a collection of entities is such that, since each cell has a product of two fitness components equal to 0 (because either survival or reproduction equals 0), only the collection (i.e. the multicellular entity) is a unit of fitness in its own right (Michod 2005; Okasha 2006; Michod and Roze 2001). Finally, along those of models the second Kantian criterion of organisms – namely, a specific relationship of parts producing themselves and the whole according to some idea of the whole – is evolutionarily realized.

Most of the theories of multilevel selection consider that some groups have to exist in order to be able to compete with other groups, so that multilevel selection is the result of both the competition between groups

31 “During the origin of each new kind of individual, conflict mediation is a necessary step, otherwise new adaptations at the new level cannot evolve, for there is no clearly recognizable (by selection) unit, no individuality. The evolution of conflict mediation is necessary for adaptation at the new level” (Michod 1999, 35).

32 See Martens (this issue) for an exposition and commentary of those models.
and the competition within groups – and it selects one type of entities scattered across various groups (Sober and Wilson 1998). For example, the various proportions of altruists in many groups will be causally relevant to the terms of the competition and a general preeminence of altruists across all groups may result from this. While, for example, studies of selfish genetic elements like autosomal killers (Burt and Trivers 2006) or t-alleles in mice (Lewontin and Dunn 1960) consider selection on two existing kinds of entities, namely alleles and organisms, here the high-level does not preexist but precisely occurs through the multilevel selection transition process. In Michod’s model, since we want to explain multicellular organisms in the first place, we cannot assume multicellular groups. So, strictly speaking, it is difficult to understand what may count in the beginning as multi-level selection. The only plausible interpretation is to consider what is most relevant here is the population structure of the set of cells. As Michod says, “During the emergence of a new unit, population structure, local diffusion in space . . . and self-structuring in space . . . may facilitate the trend toward a higher level of organization” (Michod 1999, 42). What is especially causal are effects due to the population structure. Michod models the “cost of commonness” of a rare advantageous allele and the “cost or rarity” as important causal factors that can lead to clusters of cells which would not be predicted by the pure effect of natural selection favoring the highest fitness cells.

In this sense, what matters as high level selection in the first stages of those multilevel selection models of evolutionary transition are mainly the effects of population structure upon the selective dynamics, which can mitigate the advantages of high fitness for some individual entities. To this extent, the main concepts which account for the evolution of organisms are genes, cells and population (together with population structure). The MS evolutionary theory now explains the fact of organisms; yet, far from bringing organisms within the explanatory assumptions, on the contrary it goes one step further in the MS neglect of organisms. Now, not only population and genes are accounting for evolution

33 The definition of group is difficult, and one of the main advances made by D.S. Wilson is the notion of “trait group” which distinguishes groups and the geographical or spatial cohesion of groups (Wilson and Sober 1998) – a group being the set of entities whose fitness is affected by the same circumstance in different ways, for example a set of organisms having one resource to share. But the argument given here doesn’t hang upon those considerations.

34 “Before the evolution of a structure come to ‘house’ the new higher level unit (and this must come later) interactions among lower levels units are density and frequency dependent, and, therefore, there will be problems with rarity and advantages to commonness” (Michod 1999, 35).

35 “When birth is a non linear function of density, the adaptive features of a unit of selection are no longer sufficient to predict the outcome of natural selection. ‘Survival of the fittest’ is false, and there is no measure of overall adaptedness” (Michod 1999, 72).
without a need to consider organisms, but populations (of cells) and population structures provide an explanation of the fact of organisms as an evolutionary result! The organisms – not how they function, but why they are here – are among the *explananda* of evolutionary theory, yet the widening of *explanantia* does not mean that we add organisms or organismal processes to an ontology made of suborganismal individuals (genes and cells) and populations.

Yet this evolutionary transitions program, accounting for the fact of organisms, is not the definitive answer to the critique of the role of organisms in MS. Throughout this section, I assimilated two concepts that are often taken as interchangeable in those projects, namely organism and multicellular organism. One can argue that organisms are always multicellular, but the problem is the other equation; that is, organisms are nothing but multicellularity. This is empirically false – an organism includes many symbionts, at least, and most of them are needed for its development and its functioning. So even if the evolutionary transition program provides us with the best account of multicellularity, it does not give the definitive answer to the problem of the evolution of multicellular organisms. Even if this program conceptually lies in the province of MS, its success therefore does not mean that a light expansion of MS allows a complete account of the evolutionary fact of organisms! If the evolutionary transitions program understands what is homogeneous in organisms, namely multicellularity, those are also composed of heterogeneous syntheses, especially with all kinds of bacteria, which are not among the *explananda* of such program as described here.

Some could argue that a kin-selection-based theory of host-parasite relationships could supplement the evolutionary transition program and account for what is not pure multicellularity in organisms (e.g. Van Baalen and Jansen 2001; Frank 2006). Queller (2002) talked of “egalitarian” transitions, and distinguished those from the “fraternal” ones, (i.e., involving sort of kin, like clonal cells); yet those egalitarian transitions may be understood with a broad idea of kin selection where kin selection concerns only the probability that an altruist be interacting with individuals whose probability of carrying the locus of interest is higher than average, notwithstanding all kinship and even species-belonging. Now, deciding whether this strategy will succeed, hence paving the way for a complete MS understanding of the evolutionary fact of organisms, is still an open empirical question. Actually, several scientists are doubtful about it on various grounds: either formal proofs of the weakness of cumulative gradual evolution according to MS, in the face of a com-

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36 For a philosophical account of this point, see Pradeu (2010).
positional evolution which would take symbiosis as a kind of primitive (Watson 2005); or non-neo-Darwinian theories of symbiosis (Margulis and Sagan 1986), which argue for an explanatory role of symbiosis at the basis of cellular life (namely in building mitochondria into nucleus), besides what natural selection explains. Finally, even if MS allowed a new understanding of the second Kantian criterion of organisms, by considering the specific causal binding of parts in terms of a shared evolutionary history leading to *multicellularity*, one is not yet entitled to consider such an expanded version of MS as an adequate answer to all challenges raised to classical evolutionary theory by organisms.

**Conclusion**

The eclipse of organisms during the reign of MS and the subsequent call for extending evolutionary theory in a way that would provide a place for organisms both among the explananda and in the explanatory apparatus of the theory, are manifold and I tried to show that they uncover various demands. The present investigation led to several conclusions:

- Claims for making rooms to organisms range from conceptual to empirically grounded assertions. Much of the assertions by Evo-Devo scientists are of the latter nature.
- Externalism and gene-centrism are two explanatory features of MS and are often targeted separately by the critiques of MS when they invoke the role of organisms; they are indeed logically independent.
- MS does not illegitimately neglect the level of organisms by bracketing development in many cases. The great successes of MS and of population genetics in general, occurred because the simplifications at the basis of the models – and especially, the simplifications made of organisms–were perfectly justified given the reality we wanted to model. This situation may change with the accumulation of findings both concerning small-scale biological processes (Kirschner and Gerhardt 2005) and large-scale evolution.

Finally, this means that one of the most powerful biological research projects ever broke with the conceptual geography also shared by Darwin, which used to put organisms in the center of the picture. For many explanatory purposes, MS could change this geography, and for a long time our empirical findings wholly supported this move. Ultimately, what underpins a return of organisms to the forestage of evolutionary theory are the new empirical findings, mostly in developmental fields, and, above all, when they concern relations, similarities and homologies which hold at very large scales.
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