A Phenomenological Interpretation of Organisms

by

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Abstract

In contemporary scientific theories of evolution, organisms are construed as if they were the products of genes and gene-expression. Much of our biological research operate on the assumptions that (1) organisms are reducible to and reconstructible from their genes, and (2) the organism, as a whole, is constituted by genes in a mosaic manner. The aim of my thesis is to reconsider organisms from a phenomenological point of view. I take up the question of how organisms exist by revisiting the *phenomenon* of organisms—that is, the manner in which organisms appear and show themselves—if we bracket our pre-established ways of knowing them. By suspending the usual theories and dichotomies by which we think of organisms, I show the potential of a phenomenological approach for an examination of organisms that does beyond what is available to biology as a science, or to standard philosophy of biology. Specifically drawing on the works of Merleau-Ponty, I will argue that organisms are “lived-bodies”, and that the relation they bear with their environment is one of meaning.

I begin by recounting our current scientific (mechanistic) account of organisms from the *Modern Synthesis* theory of evolution, and the position of gene-centrism within the Modern Synthesis. I then consider alternatives within scientific biology to gene-centrism, specifically, objections arising from *Ecological Evolutionary Development* and *Niche Construction Theory* in favours of a more ecological approach to evolution. Next I turn to the *Umwelt Theory* of Jakob von Uexküll, both as a secondary objection against mechanistic biology, and as an argument for the relevance of meaning in biology. Criticizing each view presented in these chapters, I argue that they are each inadequate (albeit not strictly mistaken) in their various accounts of organisms. It is lastly with the help of Merleau-Ponty that I argue we can explore a more adequate understanding of organisms and the organism-environment relation.

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Abbreviations

Works by Maurice Merleau-Ponty

SB	(1943). *The Structure of Behavior*, trans. A.L. Fischer. Boston: Beacon Press, 1963.
PhP	(1945). *Phenomenology of Perception*, trans. D.A. Landes. New York: Routledge, 2012.
NL	(1995). *Nature: Course Notes from the Collège de France*, trans. R. Vallier. Evanston: Northwestern University Press, 2003.
IP	(2003). *Institution and Passivity: Course Notes From the Collège de France*, trans. L. Lawlor and H. Massey. Evanston: Northwestern University Press, 2010.

Works by Jakob von Uexküll

TB	(1926). *Theoretical Biology*, trans. D. L. Mackinnon. New York: Harcourt
FWM	(1940, 1956). *A Foray into the Worlds of Animals and Humans, with a Theory of Meaning*, trans. J.D. O'Neil. Minneapolis: University of Minnesota Press, 2010.
TM	(1982). The theory of meaning. *Semiotica*, 42: 25-82.

Introduction — Phenomenology for biology

In our effort to understand organisms, a recurring disagreement has happened between vitalistic and mechanistic interpretations. On one side, vitalism attributes to life an internal force, which animates and distinguishes organisms from physical objects by the addition of an entelechy or vital force. On the other side, mechanism presents organisms as the working summary of their physical parts, and often reducible and reconstructable from these parts. Both vitalism and mechanism in turn have their own accounts of organic evolution—a theory of how organisms become what they are—that take on different interpretations of the organism-environment relation. For vitalism, organisms are driven to change from within, adaptive evolution is a corollary of organisms having biological impulses which manifest outwardly in the form of adaptations. Conversely for mechanism, organisms become adapted by being fitted to the external environment that pre-existing problems for survival and reproduction, in such a way that heritable and genetically grounded features are "selected" by the environment because these features confer a survival or reproductive advantage.

In this thesis I revisit the question of how it is to be an organism in an evolutionary context. To avoid confusion, my question is not about "what" it is to be an organism or "what kind of entities are organisms", but the way in which they exist (i.e. *how* they exist), such that organisms give evidence to *both* mechanistic and vitalistic interpretations. For either mechanism or vitalism to be at all convincing, they must be grounded in truths about organisms and the organism-environment relation. Moreover, given the fact that we debate between mechanism and vitalism, both indeed must have their own respective appeals. What I consider in this thesis is the *phenomenon* of organisms, which is to say, the way in which organisms (first) *show themselves*, from which later theories derive their support and evidence. My aim is to develop a position in philosophy of nature that will criticize the mechanistic account of organisms—specifically the gene-centric perspective within contemporary evolutionary biology—without at the same time becoming a version of vitalism. Often it is the case that those who participate in this debate will lean to one side of the mechanism-vitalism antithesis; instead, I purport to develop an account against mechanism that is not vitalistic in my commitments. As an alternative to the standard antithesis, I take a phenomenological approach to consider the biological significance of organisms and their *experiences* for evolution, and I offer an interpretation of organisms that focuses on their *meaningful involvement* with their environment.

To clarify what I mean by a phenomenological interpretation of organisms, first I would like to address some difficulties of the task at hand. In its usual domain, phenomenology concerns first-person lived experiences, and the way in which things are "given" or "present(ed)" in the first-person. If we understand phenomenology in this strict sense, it would be inappropriate to use it for an interpretation of the how other organisms have *their* experiences, and especially organism experiences in general. Following a strict sense of what phenomenology can do, the only experiences that we can properly investigate is our own.[1] This is then not the sense in which I will make use of phenomenology. While experience is the original content of a phenomenological investigation (and experience is always given in the first-person), interest in experience is ultimately about *meaning*. Phenomenology thus concerns the signification or sense of what is given, such that what we can consider phenomenologically is always already given in a way that is meaningful.[2] Within a particular style of phenomenology that is existential phenomenology, meaning is elaborated by considering our existential situation, and to consider meaning in this way introduces the idea of our *involvement* in the world.[3] What I borrow from phenomenology for an interpretation of organisms are these ideas of meaning and involvement.

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[1] While this includes *our* experiences of other organisms, what I wish to investigate is how other organisms have *their own* experiences.

[2] For phenomenology, meaning is both the condition and limit of sensibility, such that there can be no experience that is (of) nonsense; what is given sensibly and intelligibly is always and already given in such a way that is meaningful.

[3] As Heidegger puts it, our *being-in-the-world*.

Specifically from Merleau-Ponty, it is our existential situation of being embodied—the fact that we are *lived*-bodies, that we exist as our bodies—that shows us what it is to be meaningfully involved in the world.

The movement that characterizes a phenomenological interpretation (in both its means of criticism and positive development) is an effort to *retrieve* what is evidential about phenomena, evidence that are concealed beneath our sedimented (traditional, thematized) knowledge. As Merleau-Ponty suggests, our scientific ways of understanding often fail to realize the full implications of their own research, implications that phenomenology can draw out more explicitly. He writes,

> This is what is both exciting and exasperating in the scientist: he looks for a way to grasp the phenomenon, but he does not seek to understand it. In this way, for example in embryology, scientists glimpse a philosophy of life, but they forget what they discovered…The concern of the philosopher [i.e. phenomenologist] is to see; that of the scientist is to find a foothold… But in this attempt to get a firm grip on things, the scientist discloses more than he sees in fact. The [phenomenologist] must see behind the back of the [scientist] what the [scientist] himself does not see. (NL, 86–87)
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> Scientific thinking, a thinking which looks on from above, and thinks of the object-in-general, must return to the "there is" which underlies it; to the site, the soil of the sensible and opened world such as it is in our life and for our body—not that possible body which we may legitimately think of as an information machine but that actual body I call mine. (*Eye and Mind*, 160).

Applying phenomenology to biology, our goal is to return to the phenomena that first gave evidence to our biological theories, and once again learn from organisms as they show themselves.[4] Given that what we are concerned with is the evidential quality of *phenomena* (as that which shows itself to us), the world of perception is thus prior to any conception or idea of the world. It is on the basis of this *phenomenal priority* that our perception furnishes us with the

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[4] Merleau-Ponty writes, our aim is "to take us back to the phenomenon of which we have an experience beneath every ideology. [Our ideas] must be bracketed off and must produce [their] genealogy beginning from our actual experience." (PhP, 229)

evidence to support any idea or theory of organisms (or whatever else we chose to investigate). Before our theoretical ways of knowing something, it must first make an appearance to us, such that the way in which it shows itself grants us with the content to develop later ways of knowing.[5] If mechanistic accounts (e.g. of organisms) can be characterized by relations of cause and effect, where priority is given as causal priority, a phenomenological account can be characterized by relations of phenomenal priority. This is why phenomenology aims at returning to the level of experience, and retrieving the source of their affirmations prior to theoretical constructions that distort what appears in their appearing.

By taking a phenomenological consideration of organisms, what I want to explore is the interrogatory potential of phenomenology beyond what is available to biological science and standard philosophy of biology. If we examine the *comportment* of organisms—that is, how organisms conduct themselves in relation to their environment—organism comportment shows us a certain manner in which they exist, namely, as *lived-bodies*.[6] Using this idea from Merleau-Ponty, what I want to develop is an account that re-establishes the meaningful involvement of organisms with their environment, and I will argue that *it is as lived-bodies that organisms are meaningfully involved in the world.*

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[5] For a phenomenological interpretation of nature, Merleau-Ponty states in his *Nature* lectures that we must "look for the *justification of the idea* of Nature—that is, we must both ground its legitimacy and go beyond it by showing that it is not the only conception possible. This universe, considered in itself, refers to the *primordial* universe. The universe of theory subtends an already present universe. Behind this world, there is a more originary world, anterior to all activity, "world before a thesis": *the perceived world*. Whereas the first is given as a constructed [founded, thematized] world, the perceived [phenomenal] world is given itself in flesh and blood." (NL, 73, emphasis mine)

[6] Merleau-Ponty writes, "the behavior of another expresses a certain manner of existing before signifying a certain manner of thinking." (SB, 222)

Thesis outline

In Chapter 1, I begin by setting up what I characterize as the “mechanistic” interpretation of organisms, which is for me, an interpretation predicated on reductionism and machine-mereology (Section 1.1). Using the *Modern Synthesis* theory of evolution as our present-day example of mechanistic biology, I try to show that there is an elision of meaning in its account of organisms and the organism-environment relation. Yet despite its denial of meaning,[7] I argue that the Modern Synthesis in fact tacitly appeals to a sense of meaning in many of its concepts (Section 1.2). Within the Modern Synthesis, I further identify gene-centrism to best exemplify its mechanistic commitments (Section 1.3). By giving priority to genes and gene-expression, I try to show that (1) organisms are construed as if they are reducible to genes, and (2) in relation to the environment, both organisms and the environment exist as if they are mutually independent objects (Section 1.4).

I then consider objections within scientific biology that challenge the Modern Synthesis and gene-centrism (Chapter 2). More specifically, I appeal to findings from *Ecological Evolutionary Development* (Section 2.1) and *Niche Construction Theory* (Section 2.2) to argue for the inadequacy of mechanistic biology. Contrary to a gene-centric view of evolution, both eco-evo-devo and Niche Construction Theory argue that evolution should be examined at the level of organisms and ecology. An important phenomenon that eco-evo-deve emphasizes is *developmental plasticity*. To state its adaptive value, plasticity allows organisms to *maintain* their ways of survival and reproduction, allowing them to both buffer against and accommodate environmental fluctuations or differences. For example, I will discuss plasticity in invasive plant species that allow them the capacity to invade novel ecological settings (Section 2.3). The phenomenon of plasticity reveals an important limitation of mechanism, because it shows us the

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[7] Mechanistic biology denies meaning because meaning is subjective, whereas what is scientific must be objective.

causal entanglement between organism and environment that mechanism is unable to articulate (given its commitments to reductionism and machine-mereology). Still focusing on plasticity, I will discuss Sultan's (2015) suggestion that we can further interpret plasticity as a mode of niche construction, viz. as "*experiential* niche construction" (Section 2.3). By attending to organism experiences and acknowledging the relevance of organism experiences for evolution, we can reassess the physical, "objective" environment of mechanistic biology as the *meaningful* environment for an organism. What I bring forward from this chapter is the connection between plasticity and meaningful involvement. While we see the connection between plasticity and meaning alluded to within scientific biology, I will argue that we can better explicate the connection by a phenomenological interpretation.

Next, I turn to criticisms of mechanistic biology from Jakob von Uexküll (Chapter 3)[8], for whom mechanism was inadequate because biology proper should concern the study of biological signs and meaning.[9] With Uexküll, I try to show that we find a hint of the phenomenological interpretation I am after, namely, an account of organisms that focuses on their meaningful involvement. I first lay out Uexküll's two tasks of biology, whereby his aim was to extend the Kantian worldview by considering (1) the role of our bodies in constituting our phenomenal worlds, and (2) the phenomenal worlds of other organisms (Section 3.1). I then examine Uexküll's *Umwelt Theory*—a theory of the subjective worlds of animals, which he calls their *umwelten*—focusing on his idea of the *functional* or *meaning cycle* as the manner in which organisms relate to their context of existence (Section 3.2). From Uexküll's understanding of the organism-umwelt relation, I then discuss his rejection of Darwinian evolution in favour of the perfect and complete relation between organisms and their umwelten (Section 3.3). This is what I find to be most

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[8] Uexküll was a 19–20th century Baltic German biologist and founding figure (in retrospect) of biosemiotics—the study of signs and meaning in biology.

[9] For Uexküll, biological research properly done is the study biosemiotics. Although Uexküll precedes the Modern Synthesis and gene-centrism, I still find value in his criticisms of mechanistic biology and his development of Umwelt Theory.

problematic in Uexküll's account; as I will argue, if there is the appearance of perfect and complete fitting between organisms and their context of existence, this is because organisms actively *maintain* such a relation (Section 3.4). Given that plasticity allows organisms to maintain their meaningful relations, I argue that the phenomenon of plasticity is equally problematic for Uexküll as it is for mechanistic biology. Since plasticity is a fact of the organism body, I will argue that the source of Uexküll's problem is his understand of the organism body as a "dwelling-shell" (Section 3.4). I further take issue with Uexküll's exclusion of plants from having proper umwelten. In doing so, I think Uexküll did not draw out the full implications of his original insight which led him to develop Umwelt Theory in the first place, namely, his attention to organism comportment that attests and expresses their meaningful involvement in the world. It is then from Merleau-Ponty's account that I argue we can find a more inclusive idea meaningful involvement, one that can allows for plants to have umwelten, and admit of evolutionary change.

In Chapter 4, I draw on Merleau-Ponty's ideas of comportment (behaviour), the lived-body, and the passivity-activity relation to develop a phenomenological interpretation of organisms. For Merleau-Ponty, mechanistic biology is characterized by the "realistic analysis" of organisms that distorts their meaningful involvement with the environment; against mechanistic biology, I introduce Merleau-Ponty's *gestalt* interpretation of behaviour to clarify the manner in which organism comportment bears meaning (Section 4.1). I will then criticize Uexküll for his commitments to Kantian ontology (Section 4.2); as I will argue, insofar as Uexküll maintains the subject-object distinction inherent in Kantian philosophy, this commits him to the same premise that supports mechanistic biology which he criticized. Instead, I suggest that we find a reconciliation of the object-subject (matter-meaning) distinction by interpreting organisms in terms of Merleau-Ponty's idea of the lived-body. From this interpretation, I criticize both mechanism and Uexküll for (1) having a "congealed anatomy" of organisms that do now allow the dynamism entailed in developmental plasticity, and upholding a distinction between (2a) what is in-itself and for-itself, and (2b) passivity and activity as antitheses. (Section 4.3).

Having developed what I mean by a phenomenological interpretation of organisms, in my conclusion I will more explicitly draw out some implications for the Modern Synthesis and Extended Synthesis. I will also consider how phenomenology differs from philosophy of biology by contrasting it to Walsh's theory of *Situated Darwinism*. Lastly, I reflect on some limitations of my interpretation, and suggest possible avenues for further consideration.

Chapter 1 — The mechanistic interpretation of organisms

The *Modern Synthesis* and gene-centrism

The aim of this first chapter is to set up the content of a mechanistic interpretation of organisms which I will criticize in later chapters of this thesis. To be clear, my disagreement with mechanistic biology is not its correctness *per se*, rather, my issue is with its capacity to account for biological phenomena in a way that allows us to recognize the contributions of organism *experiences* for evolution. From a phenomenological point of view, we should first admit here that the mechanistic interpretation, as with any interpretation, depends on the "phenomenon" of organisms. Mechanism is grounded on the way in which organisms show themselves, organisms themselves present us with the content and evidence necessary for their mechanistic analysis. To argue for the incorrectness of mechanism (e.g. from vitalism) is also insufficient because we would fail to consider the fact of its scientific success. As such, my charge against the mechanistic understanding is that it presents an insufficient rather than strictly mistaken account of biological phenomena. I will argue that the limitations of mechanistic biology stem from its inadequate understanding of the organism body as a mere physical entity. By construing organisms as objects, reducible to their parts and having a "machine-mereology", the mechanistic interpretation cannot properly acknowledge the evolutionary import of organism experiences.[10] In turn, the mechanistic interpretation overlooks how organisms are *meaningfully involved*[11] with their biotic (living) and abiotic (non-living) environment (i.e. their ecological situation), where adaptive evolution can be understood as a feature and consequence of the organism-environment relation (i.e. as an ecological phenomenon).

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[10] In Chapter 4, I will argue that this is further problematic because the mechanistic interpretation—by overlooking organism experiences—also undermines its own condition of possibility, it is *because* organisms are meaningfully involved that the mechanistic interpretation can be made.

[11] The idea of meaningful involvement will be the focus of Chapters 3 and 4. I will argue that to properly consider the meaningful involvement of organisms, what we need is an alternative to the mechanistic understanding of the organism body as a *lived-body*.

In the following sections I will first specify what I mean by the mechanistic interpretation of organisms (Section 1.1). I then show how the *Modern Synthesis* theory exemplifies what I characterize as the mechanistic way of understanding (Section 1.2). This in turn leads to my discussion of gene-centrism within the Modern Synthesis (Section 1.3) as the point of arrival from mechanistic beginnings (Section 1.4). What I want to set up in this chapter (to be able to criticize in later chapters) is that the mechanistic interpretation is inadequate because it elides organism experiences and their meaningful involvement.

1.1 Reductionism and machine-mereology

Brigandt (2015) argues that we often operate with an oversimplification of what mechanistic accounts entail.[12] I agree, and to be fair, I do not hold that mechanistic accounts are strictly causal and linear, or fixed in the laws and entities they consider. While they can include ideas of feedback and dynamism against their usual stereotype, what I want to emphasize, and later criticize in my characterization of mechanism, is how it elides organism experiences and their meaningful involvement in the world. After setting up the mechanistic interpretation of organisms in this chapter, I will return to argue that meaningful experiences require a special kind of feedback (in terms of function/meaning cycles) and dynamism (of the lived-body) that the mechanistic account is unable to capture.[13]

What I problematize as the mechanistic interpretation of organisms can be characterized by two general commitments. For one, a mechanistic interpretation applies what I call a *machine-*

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[12] Brigandt writes, "Simplistic portrayals suggesting that a mechanism consists of a fixed stock of entities (that move around and interact) are erroneous in that there is the disappearance of entities and generation of novel entities. …the generation of new types of entities has to be a solid ingredient of any philosophical conception of mechanisms, given that the formation of new structures in development and evolution is a major explanatory target for developmental biology and evo-devo, respectively." (Brigandt, 2015, 25)

[13] I discuss Uexküll's idea of the function/meaning cycle in Chapter 3, and Merleau-Ponty's idea of the lived-body in Chapter 4. In Chapter 4, I further modify Uexküll's idea of the meaning cycle with insights from Merleau-Ponty.

mereology to organisms. This is a mereology modelled on the parts-to-whole relation of machines, by which the parts of an entity exist (1) *prior* to the whole, and (2) *independently* from other parts as distinct physical objects. Even when the parts assemble together, the whole remains an entity that is *partes extra partes* (parts outside of parts). A mechanistic interpretation of organisms also commits to reductionism—we can causally explain features of an organism by reducing it to its "more basic" constituents (genes), out of which the organism as a whole is secondarily re-constructible. Taking these two features together, a mechanistic interpretation of organisms is one where (1) via reductionism, organisms are relevant for evolution to the extent that they are products of their genes and products of genetic evolution; (2) via machine-mereology, the genes of an organism assemble together to form organisms in a mosaic or chimerical manner, and organisms and the environment exist independently as (and are constituted by) distinct physical objects. From this characterization of the mechanistic account of organisms, I would like to suggest that mechanism in contemporary evolutionary biology is exemplified by the *Modern Synthesis* theory of evolution, and more specifically gene-centrism within the Modern Synthesis. By its reductionist tendencies, the gene-centric account of evolution presents evolution as fundamentally a molecular phenomenon. Both biological diversity in genealogical time, and organismal development throughout the life of individuals are traced to a history of molecular changes in genes, either as random mutations that gave rise to diversity, or as differential gene expression that determines development. According to this view, organisms are containers, gene-vehicles, and "throwaway survival machines" (to borrow words from Dawkins) that confront—in a trait by trait manner—predefined selection pressures imposed by an external, self-standing environment.

1.2 Elision of meaningful involvement in the *Modern Synthesis*

Here I would like to highlight some details of the Modern Synthesis and gene-centrism by focusing on the most relevant aspects for my thesis, namely, features that distort and elide the meaningful involvement of organisms through mechanistic analyses. The Modern Synthesis (also known as the Neo-Darwinian Synthesis) is the theoretical achievement in evolutionary biology during the mid to late 20th Century; it combined (1) Darwinian evolution, (2) Mendelian and modern genetics, and (3) population genetics to form a unified account of the mechanisms of evolution.[14] Futuyma describes the Modern Synthesis as "the reconciliation of Darwin's theory with the findings of modern genetics, which gave rise to a theory that emphasized the coaction of random mutation, selection, genetic drift, and gene flow" (Futuyma, *Evolution*, G-5).[15] Again from Futuyma, the Modern Synthesis presents a theory of evolution where "adaptive evolution is caused by natural selection acting on particulate (Mendelian) genetic variations [and] population genetics—which showed that mutation and natural selection together cause adaptive evolution." (Futuyma, *Evolution*, 11)

To elaborate on these different aspects of the Modern Synthesis, Darwinian evolution refers to the theory of descent with modification by means of natural selection.[16] Natural selection is the process by which, over time, organisms become more fit in relation to their context of existence, because those with favourable variations in an environment can better survive and reproduce to pass on their traits. Darwin writes,

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[14] See Neumann-Held, "Genes–Causes–Codes" in *Genes in Development.* Prompted by the discovery of the the structure of DNA, the transition between classical to molecular genetics presents issues for what we mean by the term "gene". For classical genetics, genes were studies by mapping a phenotype (a certain appearance such as red eyes of a fruit fly) and correlated phenotypes onto certain parts of chromosomes. For molecular genetics, genes are molecular sequences of DNA.

[15] Coaction of random mutation, selection, genetic drift, and gene flow occur at the populational level, hence they are the content of population genetics.

[16] Although Darwin himself did not use the term "evolution" to describe what we now consider as evolution in his *Origin of Species.*

> As many more individuals of each species are born than can possibly survive; and as, consequently, there is a frequently recurring *struggle for existence* [emphasis mine], it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be *naturally selected*. From the strong principle of inheritance, any selected variety will tend to propagate its new and modified form. (*Origin of Species*, 5)

While our current understanding of evolution retains Darwin's original formulations of natural selection, Darwin's account did not provide an adequate theory of heredity to explain the resemblance between parents and offspring;[17] it was from Mendelian and molecular genetics that the Modern Synthesis developed its theory of heredity. The genetic components of the Modern Synthesis refer to many different discoveries and theoretical achievements that together set the foundations for our contemporary understanding. Taken together, the distinctions we introduce and the distinctions they in turn support (e.g. between genotype and phenotype, the germ-soma distinction, the direction of causation in the Central Dogma, etc.) suggest an order to the way in which evolution takes place—an order that prioritizes genes over organisms. This priority both legitimizes genetic reductionism and machine-mereology, while passing over the relevance of organism experiences and their ecological involvement. In more detail,

- Germ-plasm theory from Weismann (1892) describes the separation of the gametic and somatic cell lineages during early stages of embryological development. Germ cells (gametes) are cells that contribute to the genetic constitution of offspring, whereas somatic cells make up all other parts of our bodies—their separation we refer to as the "Weismann barrier". This distinction is important because it provides evidence at the cellular level against evolution by means of acquired characteristics, e.g. Lamarck's theory of evolution. Following the germ-

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[17] The problem with Darwin's idea of inheritance (blending inheritance) was that it failed to preserve the quality of traits—especially novel variations that were important for natural selection—without "diluting" throughout the generations. For an account of the problem of blending inheritance, see Fleeming Jenkin's (1867) review of Darwin's *Origin*.

soma distinction, changes that are incurred through an organism's experiences (e.g. losing their tails)[18] cannot contribute to evolution unless these changes were heritable through the germ-line. For instance, the germ-soma difference provides counter-evidence to the Lamarckian example that giraffes acquired their long necks (a somatic part of the body) because over generations, giraffes stretched their necks toward taller and taller trees. While this example is an over simplification of Lamarck's account, the point is that the germ-soma difference allows us to distinguish between what is relevant for adaptive evolution and what is not. The manner and extent to which organism experiences and their ecological involvement *can* be relevant for evolution is only insofar as they affect or originate in the germ line. Given that experiences take place at the somatic level (when an organism is already a body in an ecological context), the germ-soma distinction bars against the role of organism experiences for adaptive evolution. Later in Chapter 2 I will argue that this interpretation takes the embryological findings of Weismann too far in their implications, and in fact, there is some truth to evolution by means of acquired characteristics.

- In addition to the germ-soma distinction, the genotype-phenotype distinction introduces another layer of separation between the apparent organism and what really matters for evolution. *Phenotypes* describe the observable features of an organism, their bodily characteristics (e.g. eye colour) and their behaviours (e.g. nest-building), and *genotype* is the genetic source of a given phenotype. Between genotype and phenotype, the concept of phenotype already implies a causal connection between an organism's appearance and the genetic basis "for" their appearance, where genes express their phenotypes via triggers and cues from their surroundings, both from the conditions of the cell, or ecological environment at large. Adaptive evolution happens when the environment presents selection pressures that

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[18] Weismann performed cruel experiments to prove his point, he cut off the tails of mice over many generations to show that tailless mice never "evolved" from their tailless parents. The difference needed to originate in the germ (rather than somatic) cell lineage.

indirectly affect genotype frequencies through the phenotypes genes express. Continuing the line of thought already suggested by the germ-soma difference, the genotype-phenotype distinction further contributes to the elision of organism experiences for evolution. Since organism experiences are not directly "observable", experiences are not part of an organism's appearance or phenotype, and we cannot trace organism experiences to a genotypic basis; as such, we do not consider organism experiences for evolution because they cannot be studied in a way that follows the phenotype-genotype relation. Additionally, in describing organism appearance as phenotypes, we also dilute the distinction between the features of an organism and features of non-living physical objects. Later I will argue that this assimilation of organisms to mere objects is problematic because organisms "take up" their appearances (e.g. by changing themselves via developmental plasticity) in a way that matters for their evolution. I will also argue that the concept of a biological trigger for genes to express their phenotypes already (tacitly and implicitly) presupposes an idea of meaning.

The rediscovery of Mendel's works describes two key principles of genetic inheritance: the *Principle of Segregation* and the *Principle of Independent Assortment*.[19] To put them simply, phenotypic variations are heritable (i.e. yielding in the resemblance between parents and offspring) because they trace to discrete, "particulate" genes that retain their identity from parents to offspring without *blending* with other genes. This particularization of genes—and in turn, the particularization of observable features—supports a mereology that assimilates organisms to machines, both follow the same *partes extra partes* (genes outside of genes) composition of the organism or machine as a whole. Applying this machine-mereology to organisms allows us to isolate different variants of a gene (i.e. alleles)[20] and speak of the

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[19] See (Bateson, 1909). Hugo DeVries, Carl Correns, and Erich von Tschermak independently rediscovered the works of Mendel around 1900, while Mendel originally published his famous pea-plant experiments in 1865.

[20] For example, pea plants can have yellow or green alleles that determine the colour of their peas.

independent, mosaic evolution of particular genes in relation to other genes of an organism.[21] In this way, the rediscovery of Mendel's work supports an understanding of organisms as if they have the same bodily coherence as machines.[22] Later I will argue that applying a machine-mereology to organisms is inadequate, because an account of the physical body alone (as we conventionally understand it in a physicalist manner) and its machine-like assemblage do not suffice to account for the *lived*-body of organism, and it is as lived-bodies that organisms are meaningfully involved in the world.

- For the Modern Synthesis, evolutionary change is explicated in terms of changes in the relative abundance of allele frequencies in a gene population. The same conception of evolution is also used by the *neutral theory of molecular evolution*. Evolution can be neutral in the sense that what we consider as instances of evolutionary change need not be adaptive; at the molecular level, most evolutionary changes are the result of *genetic drift* in neutral genes and alleles.[23] This marks an important shift in the details of how we understand evolution. Evolutionary change is no longer understood simply as a consequence of "the struggle for existence" as Darwin had described, or differential survival and reproduction of organisms in an ecological context. Instead, evolution becomes a genetic phenomenon at the population level, and what we emphasize is *stochasticity* over the "directionality" implied by natural selection.[24] What I want to show in later chapters is that the concept of neutrality already

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[21] More specifically on mosaic evolution, every organism is a mosaic of plesiomorphic (ancestral) and apomorphic (derived) characteristics. Different characteristics (and genes) evolve at different rates, which we can infer from the fact that given common descent, any two species have some features that are unique and others in common; see (Futuyma, *Evolution*, 60-61).

[22] We also see more of machine-mereology in physiological studies of behaviour as stimuli and response reflexes.

[23] "although a small minority of mutations in DNA or protein sequences are advantageous and are fixed by natural selection, and although many mutations are disadvantageous and are eliminated by natural selection, *the great majority of those mutations that are fixed are effectively neutral with respect to fitness are are fixed by genetic drift*." (Futuyma, *Evolution*, 268)

[24] Selection is often explained in three modes, as (1) stabilizing (2) directional (3) divergent selection.

depends on the meaningful involvement of organisms in an ecological context. The neutral theory of molecular evolution in fact appeals to more than what is warranted from a strictly mechanistic account; reductionism and machine-mereology (implied by gene-centrism) are insufficient to articulate the concept of neutrality.

- The Modern Synthesis also includes our discovery of the molecular double-helix structure of DNA—which is composed of a sequence of nucleotide bases: adenine (A) guanine (G) cytosine (C) and thymine (T). Along with this came the *Central Dogma* which describes the flow of "information" in biological systems, proceeding from DNA to RNA through a process of *transcription*, and RNA to proteins through *translation,* and most importantly, never going backwards from proteins to DNA. With this discovery of the genetic code, the direction of its movement, and the fact that all life on Earth share the same basic genetic constitution,[25] we further support the reductionism of organisms to their genes, especially since we can trace differences between organisms in terms of differences between their genomes. Moreover, given that genes are inherited independently from each other (although with occasional linkage), the organism as a whole can be studied in a part by part manner by isolating and inducing genetic mutations. Once we understand the genetic code in terms of nucleotide bases, we can clarify various kinds of mutations by the specific changes to a DNA sequence,[26] and in turn manipulate genes to understand their effects (e.g. we can negatively infer the effects of a gene by knocking it out). Later I will show that genetic/molecular manipulations are in fact inadequate for what they aim to understand—namely, organism "traits" and

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[25] This is also taken as further support for Darwin's theory of common descent and evolution as descent with modification.

[26] For example, change at single nucleotide base pair (or in classical genetics, a change that maps to a single gene locus) is called a *point mutation*. Point mutations from purine to purine (A–G) or pyrimidine to pyrimidine (C–T) are called *transitions*, and point mutations between purines and pyridines (e.g. A–T) are called *transversions*. Mutations that do not make a difference for the amino acid sequences translated from RNA are called *synonymous* mutations, whereas *non-synonymous* mutations change the translated amino acid, although not necessarily affecting the overall phenotype of the organism.

evolution of their traits. What we should recognize is that the potential or disposition of a gene is a contextual phenomenon. Situated in the context of the organism as a systematic whole, genes *obtain* their functions such that we can study them by means of inducing mutations. The negative understanding of gene function (by removing a gene) is problematic because we can equally argue that what we in fact study is how *organisms* accommodate their genomic differences, rather than the specific effects of modifying any gene in particular. In a sense, these studies also lack objectivity because what we examine are the "laboratory organisms" removed from their ecological, hence evolutionary context. Despite the detailed ways in which we can manipulate genomes, without considering the meaningful involvement of organisms, we cannot properly understand how genetic changes play out in a natural eco-evolutionary context.

From these different components of the Modern Synthesis,[27] what I hope to emphasize are its mechanistic (again, reductionist with a machine-mereology) commitments and tendencies that contribute to the elision of organism experiences and their meaningful involvement. Evolution takes on a movement beginning from genes to the organisms they produce. Organisms are presented as epiphenomena, whereas genes are the true drivers of evolution, and as such, the proper object of interest for evolutionary research. Following a series of distinctions that support the fundamentality of genes, our modern understanding of evolution is such that organisms are no longer its proper candidate. Gene-centrism is the point of arrival for both the reductionism and machine-mereology of a mechanistic interpretation.

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[27] For a pluralist interpretation of the Modern Synthesis, see Love, "Rethinking the Structure of Evolutionary Theory for the Extended Synthesis" in *Evolution: The Extended Synthesis.*

1.3 Gene-centric view of organisms and the environment

In this section I would like to elaborate on the different components of gene-centrism to further demonstrate how it contributes to the elision of meaningful involvement. From Robert's (2004) articulation of gene-centrism, we can distinguish between genetic informationism, genetic animism, and genetic primacy—of these I will discuss genetic informationism and primacy.[28] I will also discuss Dawkins' theory of *Extended Phenotype* as a gene-centric interpretation of the environment.

1.3.1 Genetic informationism and genetic primacy

Genetic informationism is the idea that "genes contain the entirety of the preformed, species-specific evolutionary and developmental information [to make organisms]."[29] Genes inform the development of organisms in a way that we can know, *a priori*, the developed organism as a whole on the condition that we figure out which and when genes are expressed. If it is proximally through development that organisms become what they are, development is ultimately a matter of developmental genetics and gene expression; hence, from our knowledge of genes we can then compute and decode organisms from their genomes. Given genetic informationism, an organism's ecological involvement at best plays the role of enabling conditions for gene expression. Organism experiences within their ecological situations are contingent epiphenomena that do not (and in principle, cannot) introduce any new relevance for their evolution, genes already contain the information to and from which we can reduce and regenerate the organism.

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[28] I do not discuss genetic animism because I think it is entailed in genetic informationism. Genetic animism is the ideas that there are a genetic "programmes" in DNA responsible for the development of an organism. Genes animate (coordinate and systematize, i.e. *inform*) developmental mechanisms to form a unified and coherent organism.

[29] (Robert, *Embryology, Epigenesis, and Evolution*, 118).

Likewise, genetic primacy is the idea that genes as parts exist before the organism as a whole, further supporting the machine-mereology of a mechanistic understanding. We can distinguish this priority in terms of historical and developmental priority. Genes have developmental priority because they are causally responsible for programming the way in which organisms unfold from their molecular basis. In the developing embryo, the genome of an organism exists causally before the developed organism (i.e. organisms we see in the world), and differences between genomes explain the observable differences between individual organisms (and of course, differences between species). Lewontin gives the analogy of developing a photograph to describe this genetic paradigm, where genes are the negative film of an already fully captured image, organisms are the photographs, and the environment is the chemical bath that enables film to be expressed.[30]

By the same token, genes also have historical priority because molecular replicators and organic molecules (as objects of chemistry) are thought to exist before what we now consider as organic life (objects of biology). In the story of life on Earth, life is thought to have emerged in a "primordial soup"—a heterogenous mixture of molecules, some of which were able to replicate themselves. By chance, mutations (which arose either by mistakes in replication or via environmental factors such as UV rays) gave rise to a *variety* of replicators that were then subject to molecular evolution. Given that resources (e.g. nitrogen) for self-replication were limited, or at least became limited over time, there was then *competition* between replicators.[31] Replicators that were able to destroy others and protect themselves, e.g. through a hydrophobic membrane, persisted in place of those that lacked a protective membrane—these entities we now consider as

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[30] Lewontin says, "Modern developmental biology is framed entirely in terms of genes and cell organelles, while environment plays only the role of a background factor. The genes in the fertilized egg are said to determine the final state of the organism, while the environment in which development takes place is simply a set of enabling conditions that allow the genes to express themselves, just as an exposed film will produce the image that is immanent in it when it is placed in a chemical developer at the appropriate temperature." (*The Triple Helix*, 4)

[31] Competition here does not depend on a concept of volition or conscious intentionality.

the first "cells" and life on earth. Over time, replicator populations naturally tended towards a greater number of individuals with (1) higher accuracy of replication, (2) greater longevity, and (3) higher fecundity; *natural selection* is the mechanism by which we arrive at replicators with at least one of these three modes of persistence and stability.[32] In this story of life on Earth, all the components of Darwin's theory of evolution (heredity, variation, competition) are exemplified at the molecular level prior to the origin of "life"; it is in this sense that genes have historical priority over organisms. If we accept that this story of genetic primacy *already* articulates what is essential about the workings of evolution, there is no further contribution by including organisms because organic evolution can already be explained at the molecular level.

1.3.2 Gene-centric view of the environment

Some authors take the gene-centric narrative a step further to construe the environment itself as a genetic achievement. In *The Extended Phenotype*, Dawkins argues that even aspects of the physical environment (e.g. a beaver dam or bird nest) can be interpreted in terms of "extended phenotypes" of genes, which are important for evolution by virtue of their genetic basis. His idea is that our understanding of phenotype (again, the observable characteristics of an organism) should not be limited to the immediate body of organisms, but *extended* to all genetic achievements both inside (bounding) and outside (surrounding) organisms. While genes are bound to their organism-vehicles and do not exist freely in the world, for Dawkins, this does not further necessitate that the phenotypic *products* of those genes also exist as part of the organism body. This is why Dawkins refers to his theory of extended phenotype as "action at a distance", he writes,

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[32] (Dawkins, *The Selfish Gene*, 16-18).

> And how far afield can the phenotype extend?…The farthest action at a distance I can think of is a matter of several miles, the distance separating the extreme margins of a beaver lake from the genes for whose survival it is an adaptation.[33] If beaver lakes could fossilize, we would presumably see a trend towards increased lake size if we arranged the fossils in chronological order. The increase in size was doubtless an adaptation produced by natural selection, in which case we have to infer that the evolutionary trend came about by allele replacement. In the terms of the extended phenotype, alleles for larger lakes replaced alleles for smaller lakes. In the same terms, beavers can be said to carry within themselves genes whose phenotypic expression extends many miles away from the genes themselves. (*The Extended Phenotype*, 233)

Taking a gene's eye view of evolution, even features of the physical environment, although proximally traceable to organism behaviours (e.g. nest building or dam building), can ultimately be considered genetic in their proper evolutionary origin. Here I would like to examine the evidence from which Dawkins argues in favour of his theory.[34] In his earlier work *The Selfish Gene*, Dawkins argued that certain animal behaviours, specifically the evolutionarily problematic behaviour of altruism,[35] only make sense if we interpret them from a gene-centric perspective. Behaviours such as altruism *can* evolve (i.e are evolutionarily possible) because they tend to maximize *inclusive fitness*—a measure of fitness that takes into account the common genes shared between individuals.[36] What this means is that animals will evolve certain behaviours because

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[33] Dawkins is referring to the dam constructing behaviour of beavers that result in the blocking water flow to make up beaver lakes. This is supposed to be advantageous for beavers because it allows them more space for swimming (their preferred mode of locomotion).

[34] Dawkins says, "It will be remembered that the 'central theorem' of the selfish organism claims that an animal's behaviour tends to maximize its own (inclusive) fitness. We saw that to talk of an individual behaving so as to maximize its inclusive fitness is equivalent to talking of the gene or genes 'for' that behaviour pattern maximizing their survival. We have now also seen that, in precisely the same sense as it is ever possible to talk of a gene 'for' a behaviour pattern, it is possible to talk of a gene, in one organism, 'for' a behaviour pattern (or other phenotypic characteristic) in another organism [or another entity in general]. Putting these three things together we arrive at our own 'central theorem' of the extended phenotype." (Dawkins, *The Extended Phenotype*, 233)

[35] Altruism is evolutionarily problematic because in an altruistic population, selfish individuals (self-genes) can easily displace the altruist population. Before altruism (as a trait) can propagate in a population, selfish individuals will always tend to displace altruistic ones.

[36] Inclusive fitness is most likely between relatives (as a corollary of heredity), although the idea of inclusive fitness can apply to any two individuals that have genes in common.

those behaviours increase the number of genes "for" that behaviour in a population, whether or not those genes are bound within an individual organism-vehicle. For Dawkins,

> the ordinary logic of genetic terminology leads *inevitably* to the conclusion that genes can be said to have extended phenotypic effects, effects which need not be expressed at the level of any particular vehicle. (*The Extended Phenotype*, 196, emphasis mine)

If we accept the arguments for the primacy of genes, we can extend the idea of phenotype (as the expression of a genotype) even to parts of the physical environment; not only are organisms themselves genetic products, the environmental *niches* they construct through their behaviours are also genetically grounded.[37] By altering or producing the physical environment as their extended phenotypes, genes can further improve the circumstances of their propagation beyond the boundary of its organism-vehicle.

Looking ahead, I will argue that this account is problematic because by rendering the environment as a genetic product, I think we elude the fact of meaningful involvement if we undo the organism-environment difference in this manner. While Dawkins may shift the *boundary* between organism and environment, he does not reconfigure their relation in the way I envision. Upon closer examination, Dawkins' account of the extended phenotype does not in fact do away with the organism-environment dichotomy; the extended phenotype does not challenge the narrative of the "selective environment", but shows us the extent of its influence. Indeed, there remains an impervious "outside" which selects genes via their phenotypes, even when phenotypes reach beyond their immediate container (the organism) and manifest as features of the physical environment. Although my aim is also to blur the organism-environment distinction as independent objects, their difference requires that we do not counteractively render the environment as another expression of genes. In the chapters that follow I will argue that organisms and the environment cannot be separated or articulated in a way without fundamental overlap, ambiguity is at the heart of their relation.

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[37] I discuss the concept of a biological niche and niche construction in Chapter 2.

1.4 Independence of organism and environment

As we have seen, the "environment" of the mechanistic account is something that presents both enabling conditions for the proper expression of genes, and selection pressures to which genes provide solutions through their phenotypes. While Dawkins' idea of the extended phenotype shifts the boundary between organism and environment by rendering the environment as yet another expression of genes, I suggest that whenever we follow a machine-mereology of organisms, we necessarily maintain the organism-environment distinction. This can be best exemplified by the *adaptationist programme* in evolutionary biology.[38] For an entity that is *partes extra partes* (traits outside of traits, genes outside genes), the machine-organism is also individuated from the environment as distinct physical objects. Further implicit here is the idea that the environment itself would exist all the same without organisms inhabiting or experiencing it. Working with assumptions of machine-mereology, we support the organism-environment distinction by an account of how adaptations occur. When we say that adaptations are the result of environmental factors imposing selection on organism features, it is as if organisms and the environment are stand-alone objects, and as if features of an organism exist isolable from other features, each of them independent of the organism as a whole.

The *adaptationist programme / Panglossian paradigm*—in a word, adaptationism—clearly implicates the machine-mereology of organisms, keeping an "objective" distinction between organism and environment as if they relate to each other like filling to a pre-established mould. For adaptationism, "an organism is atomized into 'traits' and these traits are explained as structures optimally designed by natural selection for their functions" (Gould & Lewontin, 1979, 585). As Gould and Lewontin famously articulated and criticized, adaptationism refers to the tendency in evolutionary biology to interpret each and every feature of organisms as a product of natural selection, or adaptive "solutions" to environmental "problems". While Darwin only argued

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[38] Therefore including Dawkins' account.

for a sufficient connection between natural selection and the phenomenon of "good fit" between organisms and the environment, for adaptationism, good fit is also taken as a necessary condition for inferring natural selection. This is to say, from the phenomenon of good fit, adaptationism infers that natural selection has occurred, such that *every* feature of an organism is an adaptation, actually or hypothetically.[39] Gould and Lewontin note that even when it is unclear how certain features are adaptive, evolutionary biologists would tell *adaptive stories* supporting the adaptive value of said feature. Evolutionary biologists further introduced the idea of an "evolutionary trade-off" to explain the *lack* of trait-by-trait optimization of organisms. If there is sub-optimality, this is because there are evolutionary trade-offs—in which case the organism as a whole is the best *compromise* between various traits and competing or divergent selection factors. For example, we can see the adaptationist way of thinking in E.O. Wilson's account of certain human society's disposition for carnivory, including ancient Aztec cannibalism as an unconscious adaptation for our dietary need of protein, or a "solution" (among other possible solutions) to the "problem" of sustaining our nutritional needs given limited environmental resources (Wilson, 1979).

Since my aim is to develop a phenomenological interpretation of organisms, I will not be giving a traditional refusal of adaptationism even though I agree with the objections.[40] Instead, what I want to show is that adaptationism already appeals to concepts beyond what a mechanistic interpretation can allow, and without which it would be inadequate for its own explanations (viz. the adaptive organism-environment relation). From Wilson's example of cannibalism, what we

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[39] Gould and Lewontin write, "We fault the adaptationist programme for its failure to distinguish current utility from reasons for origin…for its unwillingness to consider alternatives to adaptive stories; for its reliance upon plausibility alone as a criterion for accepting speculative tales; and for its failure to consider adequately such competing themes as random fixation of alleles, production of non- adaptive structures by developmental correlation with selected features (allometry, pleiotropy, material compensation, mechanically forced correlation), the separability of adaptation and selection, multiple adaptive peaks, and current utility as an epiphenomenon of non-adaptive structure." (Gould & Lewontin, 1979, 581)

[40] See (Gould & Lewontin, 1979), (Lewontin, 1979), and (Lewens, 2009) for arguments against adaptationism.

overlook is the fact that organism are involved in the world with relations of meaning, thereby excluding social or cultural meaning as an adequate or proper explanation for cannibalism. When Wilson (and to speak of adaptationism in general) reduces the phenomenon of cannibalism as a "solution" that alleviates a hypothetical "problem" of nutrition, we are already tacitly appealing to (or at least attuned to) a sense of *meaning*; the problem-solution relation itself requires that they address each other in a meaningful way. The point of my phenomenological consideration is to make the appeal to meaning in biology more explicit.

Along the same lines of argument against Dawkins' theory of the extended phenotype, adaptationism is problematic because it elides organism experiences and their ecological involvement. Again, my aim is not to erase the organism-environment difference, if we hold that there is no meaningful distinction between organisms and the environment, it would never make sense to speak of their separation in the first place. From the fact that we *can* recognize organisms and the environment in a distinctive manner (albeit insufficiently from the mechanistic formulation), taking a phenomenological perspective, the goal is to explore the organism-environment difference without going so far as to either (1) "internalize" the environment as a product of gene expression, e.g. Dawkins' extended phenotype, or (2) "externalize" the environment from organisms as a separate and impervious entity, e.g. adaptationism. From gene-centrism and adaptationism, organisms and the environment are brought either too close or too far apart, neither of which allow for the meaningful involvement that requires a specific kind of difference and unity that we cannot articulate from a mereology of "objects outside of objects". What we need instead is an *organic mereology* which I will explore in Chapter 4.[41]

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[41] Merleau-Ponty describes an organic mereology between the lived-body and the world, he writes "One's own body is in the world just as the heart is in the organism: it continuously breathes life into the visible spectacle, animates it and nourishes it from within, and forms a system with it." (PhP, 209)

Conclusion 1

Above I have tried to set up what I will criticize as the "mechanistic" interpretation of organisms, which is characterized by reductionism and machine-mereology. I have tried to explore how different aspects of our contemporary understanding of organisms eclipse the phenomenon of their meaningful involvement.[42] Following reductionism and machine-mereology, gene-centrism is our point of arrival from mechanistic beginnings, whereby organisms receive their significance only when assembled out of genes as a mosaic entity that is *partes extra partes*. The fitness of organisms to their environment, tracing a history of how they came to be, also depends on the history of changes in allele frequencies at the populational level. Organisms themselves are only transient survival-machines through which genes carry out their persistence. To summarize gene-centrism with a quote from Dawkins,

> The individual bodies are still there; they have not moved, but they seem to have gone transparent. We see through them to the replicating fragments of DNA within, and we see the wider world as an arena in which these genetic fragments play out their tournaments of manipulative skill. Genes manipulate the world and shape it to assist their replication. It happens that they have 'chosen' to do so largely by moulding matter into large multicellular chunks which we call organisms, but this might not have been so. Fundamentally, what is going on is that replicating molecules ensure their survival by means of phenotypic effects on the world. It is only incidentally true that those phenotypic effects happen to be packaged up into units called individual organisms. (*The Extended Phenotype*, 4-5)

In the chapters that follow I will criticize mechanistic commitments from different perspectives of the *Extended Synthesis* in Chapter 2, Uexküll's *Umwelt Theory* in Chapter 3, and the phenomenological interpretation of organisms that I develop in Chapter 4. These chapters will

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[42] To reiterate, this includes both a genetic reductionism of organisms to genes, and the idea of a self-standing environment if not the achievement of genes as extended phenotypes) which imposes selection pressures that affect gene frequencies in a population. Even for Dawkins' idea that the environment is a genetic achievement, it is still a phenotype that came to be through selection pressures from a previously existing environment (prior to the niche).

increasingly emphasize the fact that organisms are meaningfully involved in relation to their contexts of existence.

Chapter 2 — Scientific criticisms of mechanistic biology

T*he Extended Evolutionary Synthesis:*
Ecological Evolutionary Development & Niche Construction Theory

In the context of a mechanistic, gene-centric view of evolution, organisms become secondary phenomena and residues that remain unaccounted for, only to be cast out of evolutionary theory. Before considering objections from philosophy, in this chapter I examine criticisms within scientific biology that challenge the mechanistic account of organisms and evolution. Here I draw on the *Extended Evolutionary Synthesis*—specifically, I will discuss *Ecological Evolutionary Development* (eco-evo-devo or EED for short) and *Niche Construction Theory* (NCT) within the Extended Synthesis to establish the content for my later phenomenological interpretation organisms, in a way that is informed by contemporary scientific research.[43] The common goal of EED and NCT is to expand our understanding of evolution by emphasizing the role of organisms and ecology for evolution. Rather than presenting evolution as a genetic or molecular phenomenon, proponents of EED and NCT argue that evolution is not merely the change of gene (allele) frequencies in a population, it concerns organisms, their development, and development that is always situated in an ecological context. While EED rejects the reductionism of mechanism by demonstrating the inadequacy of the one-to-one correspondence between phenotype and genotype, NCT provides an alternative to the separation of organisms from the environment by showing how organisms themselves realize their "selective environment". From EED and NCT, organisms are neither predefined by their internal genetic constitution, nor by forces from an

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[43] In their scientific reception, eco-evo-devo and Niche Construction Theory has prompted some biologists to shift toward an alternative conceptual framework than the Modern Synthesis, which they refer to as the *Extended Evolutionary Synthesis*. See (Laland *et al*., 2015) for more detail on the Extended Synthesis and its relation to the Modern Synthesis theory of evolution. To name a few points of difference, the Extended Synthesis emphasizes (1) the reciprocal causation between organism and environment, (2) a more inclusive idea of inheritance that expands the mechanism of inheritance beyond its genetic component, (3) the contributions of organism development for phenotypic variation (where variation is still the "raw material" of evolution), and most generally (4) the shift in focus from genes to organisms for evolutionary theory.

external environment; instead, what they positively emphasize is the significance of causal feedback in the organism-environment relation.

To cover each direction of the organisms–environment relation, EED (Section 2.1) focuses on the way in which the environment influences organisms, with particular attention to the phenomenon of *developmental plasticity* and norms of reaction, which maps the developmental repertoire—hence, adaptive repertoire—of organisms under different environmental conditions. Developmental plasticity will be a recurring phenomenon that I discuss in later chapters. In turn, the task of NCT (Section 2.2) is to examine the role of organisms on the environment. Proponents of NCT argue that

> just as the environment participates in shaping the organism, the organism's presence, activities, products, and byproducts modify its environment. By virtue of those environmental modifications, organisms influence their own functional and selective circumstances and, through effects on shared habitats, those of cohabiting neighbours. (Sultan, *Organism and Environment*, xiii)

Drawing on both EED and NCT, the positions I clarify in this chapter will criticize the mechanistic interpretation for its exclusion of organisms from evolutionary theory. More precisely, I will argue that mechanistic biology is insufficient because it neglects the fact that organisms *experience* their environment, and in turn, the relevance of organism experience for evolution (Section 2.3). What I introduce in this chapter is the manner in which a preliminary attention to organism experience and meaning are presented as *scientific* objections against mechanistic biology. However, staying at the level of science, the theories I consider in this chapter challenge mechanism without questioning or surpassing the common assumptions they share as "scientific" objections. In this case, my later phenomenological account contributes to the discussion of organisms in ways that scientific biology cannot. In Chapters 3 and 4, I will reinterpret the biological significance of organism experiences and meaning in terms of Uexküll's *Umwelt Theory* (feedback in terms of meaning-cycles), and Merleau-Ponty's idea of the *lived-body*.

2.1 Ecological Evolutionary Development

Similar to developmental genetics, Ecological Evolutionary Development (EED) also investigates the question of how organisms become what they are, albeit with explanations at the level of organism development rather than genes. While developmental genetics assumes the priority of genes for explaining ontogeny and its adaptive value, including the concept of heredity, EED focuses on *developmental systems* to explain the same phenomena; by developmental systems, I refer to "the matrix of resources that are required to reproduce the life cycle" of an organism (Griffiths & Hochman, 2015, 1). Not accepting genetic primacy and genetic informationism, for proponents of EED, evolution is not a measure of changes in allele frequencies in a population, it depends on changes to the system of genetic, epigenetic, and developmental factors on part of organisms, all of which are situated in an ecological context that together establish the conditions of adaptive evolution.

2.1.1 Epigenetics, genetic assimilation, and canalization

- Contrary to the conclusions that Weismann drew from his embryological research,[44] *epigenetics* allows us to challenge the evolutionary conclusions that Weismann (and in general, gene-centrism) drew with regard to the germ-soma distinction.[45] To reiterate, Weismann observed that in the developing embryo, gametic and somatic cell lineages are separated early on in the process of embryogenesis, and given that only the germ-line contributes to the genetic constitution of future generations, Weismann concluded that events at the somatic level have no bearing on evolution. From studies in epigenetics, support for

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[44] I discussed Weismann's germ-plasm theory in Section 1.2

[45] Epigenetics can include changes to the structure of a gene without changing its molecular sequence, such as *DNA methylation* that prevents a gene from being expressed by the addition of a methyl group, or *histone modifications* that affect the proteins (histones) to which DNA is bound in its condensed form (Jablonka & Raz, 2009).

genetic primacy and informationism from Weismann's research is not as strong as gene-centric biologists take it to be. Despite the separation of gametic and somatic cell lineages, by means of epigenetic inheritance, somatic changes can in fact contribute to what is heritable; epigenetic studies show us that there is indeed some truth to evolution by means of acquired characteristics or Neo-Lamarckian evolution. For example, in Agouti mice (Morgan *et al*., 1999), between monozygotic twins, the sibling with DNA methylation at the *agouti* gene tend to have brown fur and are thin, whereas the sibling without a methylated *agouti* gene have yellow fur, are prone to obesity, diabetes, and increased susceptibility to tumours. Interestingly, whether or not individuals have methylated *agouti* genes depend on the diet and nutrition of their mothers—pregnant mice that had diets rich in folic acid tend to have offspring with methylated agouti genes. Regarding this example, the gene-centric account is limited because genetic changes alone are unable to account for the phenotypic differences between twins. If we further consider the evolutionary significance of their different phenotypes, a genetic explanation is inadequate to explain the advantage or disadvantage between methylated and non-methylated *agouti* genes. While Weismann revealed embryological details that contribute to the mechanisms of heredity, we should remember that the cellular biology of heredity (or even its molecular chemistry at the DNA level) does not exhaust heredity in its evolutionary significance. In its evolutionary significance, heredity is about the resemblance between parents and offspring, and the faithful reproduction of characteristics between generations. Contrary to the restrictions of the Weismann barrier, epigenetics and EED show us that heritable variations of organism appearances (and if they are selected, adaptions) need not originate at a gametic or molecular-genetic level,[46] somatic-

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[46] In this case, what we mean by genetic is limited to the molecular sequence of DNA, while DNA methylation or histone modifications also deal with the modification of genes, they are distinguished as *epi*genetic.

level contributions such as diet and nutrition matter for adaptive evolution in a significant manner.

- It is because *developmental systems* are highly coordinated that we have certain adaptations such as tool use. Tool use is hypothesized to have co-evolved with the evolution of bipedalism, or even its byproduct (Rolian *et al.*, 2010). Since the development of our hands and feet are highly coordinated, changes to the development of one affect the development of the other. From structural changes in our feet for bipedalism and endurance running (strengthening and distal extension of the big toe and shortening of the lateral digits),[47] these changes, when applied to the development of our hands, allowed for precision grip necessary for tool use.[48] What this example shows us is that development too can be the source of adaptive evolution, contrary to genetic primacy. More than genetic changes, adaptation depends on the evolutionary development of an organism, and development that takes place given an organism's ecological context of existence.[49]

- With the phenomenon of *genetic assimilation*,[50] we know that adaptive phenotypes need not originate from changes in the genome. Adaptive phenotypes can arise *first* through changes in developmental systems, and only later do genes—which may further secure these developmental pathways—come to be. Since we can only identify adaptations *after* they have occurred, we are led to study the mechanisms of adaptation in a backwards manner. If there are genes that correlate to certain modes of development, even if these genes came after

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[47] We can visualize these changes if we compare our hands and feet to our tree-climbing primate relatives.

[48] For a more detailed description see (Walsh, *Organisms, Agency, and Evolution*, 175-176).

[49] As Walsh puts it, "the capacity of a population to undergo adaptive evolution is grounded in the capacities of organisms, particularly those… that are manifested in their development: modularity, plasticity, robustness, innovation. These are all features of the adaptiveness of individual organisms." (*Organisms, Agency, and Evolution*, 152)

[50] See (West-Eberhard, 2003), (Palmer, 2012), and (Pigliucci *et al.*, 2006).

developmental changes, they still receive an appearance of priority when we begin from gene-centric assumptions. Genetic primacy takes for granted, and therefore does not acknowledge, the *retroactive* significance of genes when it identifies sequences of DNA as the “genotype” responsible for “phenotypes” which actually originated developmentally. EED shows us that the “information” of development is not encoded in the molecular genome, but distributed throughout the entire developmental system. Development does not depend on a single locus of origin and control, instead, developmental outcomes are contingent upon the context in which development occurs (Griffiths & Hochman, 2015).

- We know that genetic mutations are a common occurrence, they are always accumulating in our genetic constitution, and most mutations that take effect tend to be harmful or deleterious. Nevertheless, we do not observe their possible effects nearly as much as the occurrence of mutations themselves. This is because development is *canalized* in a way that buffers the effects of mutations, developmental systems can accommodate changes in the genome without causing harm at the level of the organism.[51] Hence, genes themselves do not exist in a *partes extra partes* manner from other genes, the impact of a gene or mutation depends on the systematicity of development as a whole. Without the prior systematicity afforded by development, the adaptive value of genes and genetic mutations would never obtain.

2.1.2 Developmental plasticity

One of the key limitations of the mechanistic accounts is that it cannot explain adaptively *plastic* features, i.e. phenotypes that are developmentally flexible in a way so as to benefit an organism in their survival and reproduction. To quote West-Eberhard,

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[51] For more on the phenomenon of canalization see(Waddington, 1956, 1957, 1966), and (Brigandt, 2015).

> In modern evolutionary biology there is still a gap between the conclusions of a genetical theory for the origin and spread of new traits, and the observed nature of the traits being explained, the manifest phenotypes, always products of genes and environment. This gap is especially clear in discussions of adaptively flexible [i.e. plastic] morphology and behaviour. (*Developmental Plasticity and Evolution,* 3)

Plasticity describes the capacity of an individual to develop differently relative to their conditions of existence. For example, genetically identical water fleas (*Daphnia)* that receive predator cues will develop helmet-shaped exoskeletons, compared to individuals that do not receive predator cues and do not develop helmets (Figure 1).[52]

Figure 1. Developmental plasticity in genetically identical water fleas (*Daphnia*), in the presence (left) and absence (right) of their predator chemical cues. Retrieved from (Agrawal, 2001).

Instead of designating fixed phenotypes to organisms on the basis of their genotype, the fact of plasticity requires us to understand the appearance of organisms in terms of their *norms of reaction*—a function of phenotypic expression (of the same genotype) against different

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[52] Later I will argue that the possibility of there being “predator cues” depends on *Daphnia* having meaningful relations with their context of existence, a context that includes other organisms as their “predator”, and signs that indicate their predators in the form of a molecular “cue”.

environmental backgrounds.[53] Against the reducibility of organism appearance to genotype (which is already presupposing their one-to-one correspondence), genotype-phenotype relations tend to be highly variable depending on the ecological conditions in which organisms exist.[54] Plasticity establishes a causal impact from the environment to the developing organism, that is, plasticity shows us that organism development synchronizes with environmental fluctuations in ways that better accommodate their survival or reproduction (Gilbert *et al.*, 2015). Genes alone do not provide the "information" for the appearance of organisms, the source of this information is distributed throughout the systems of development. From EED, there is both a role for genotype and phenotype in providing the resources for adaptive evolution; to trivialize or reduce one to the other only gives us a partial, hence, insufficient understanding.

The phenomenon of developmental plasticity will be a common thread throughout the remaining chapters of my thesis. For now, it will also link my discussion of EED to *Niche Construction Theory* (NCT). As a key phenomenon that shows us the limitations of gene-centrism, plasticity is not only important for evolutionary development; we can further elaborate its significance as a mode of niche construction.

2.2 Niche Construction Theory

Niche construction is a concept that brings together different activities of organisms that result in the modification of their environment, often in ways that improve their chances of survival or reproduction (i.e. their fitness) within their created niche (Odling-Smee *et al.*, 2003). Although organisms are subject to selection pressures from the physical environment, NCT emphasizes that organisms are not passive in this relation, theys actively construct and contribute to their

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[53] In other words, a norm of reaction maps out the *developmental repertoire* of an organism given its genetic constitution.

[54] In the other direction, a single phenotype can also trace to many different genotypes by convergent evolution.

ecological situation, which in turn filters the "selection factors" that apply to them. Lewontin and Levins write,

> A living organism at any moment in its life is the unique consequence of a developmental history that results from the interactions and determinations by internal and external forces. The external forces, what we usually think of as "environment," are themselves partly a consequence of the activities of the organism itself as it produces and consumes the conditions of its own existence. Organisms do not find the world in which they develop. They make it. Reciprocally, the internal forces are not autonomous, but act in response to the external (Lewontin & Levins, *Biology Under the Influence,* 242).

The environment does not confront organisms with pre-existing problems to which they passively become fitted over time. Contrary to the adaptationist account of evolution I discussed in Chapter 1, evolution is not a process whereby organisms are selected to solve pre-established environmental problems. For example, by constructing dams, beavers dramatically alter the ecological and evolutionary context of their existence.[55] The effects of a beaver's dam further cascade throughout the entire wetland ecosystem, affecting nutrient cycles, species richness, community structures, etc..[56] This is why some biologists also refer to niche construction as "environmental engineering" and speak of its effects in terms of "eco-evo feedbacks" (Sultan, *Organisms and Environment*, 37n2).

As Odling-Smee *et al.* note, "that organisms engage in niche construction is beyond dispute, but whether this niche construction makes any substantive difference to the world in which they live, or to ecological and evolutionary processes, is open to debate" (Odling-Smee *et al.*, 2003, 36). To address this concern with an example, one of the most important instances of an organism changing the environment at large is the Great Oxidation Event.[57] In the oxygenation history of Earth's atmosphere and oceans, ancient cyanobacteria (blue-green algae) were some of the first

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[55] The more direct effect of building dams is to protect themselves from predators.

[56] For more on beaver dams and niche construction, see (Naiman *et al.* 1988).

[57] For more on the Great Oxidation Event, see (Lyons *et al.*, 2014).

organisms to produce free oxygen (O_2) by means of photosynthesis.[58] The oxygen they produced initially reacted with dissolved iron in the oceans and formed iron-oxide (rust) deposits that settled at the ocean floor. As cyanobacteria continued to produce more oxygen, free iron became less available in the oceans, and oxygen began to release into the atmosphere. Over time, the photosynthetic activity of cyanobacteria transformed Earth's oceans and atmosphere to one that is rich in oxygen. This change promoted the diversification of organisms capable of using oxygen (aerobic organisms), while simultaneously bringing about the extinction of many anaerobic organisms, organisms that dwell in low oxygen or oxygen-free environments.[59] With this example, we see organisms *co-evolving* with their environment as aerobic organisms themselves perpetuate the conditions that allow for their diversification. What this example of the Great Oxidation Event calls attention to is the fact that organisms have decisive effects on the environment at large; their mere presence can bring about ecological evolutionary feedbacks to their surroundings (including other organisms).[60] In addition to organism that "actively" modify their environment through niche constructing *behaviours*, simply by existing, organisms engage with the environment in ways that matter for ecology and evolution.

Contrary to the machine-mereology of mechanism, niche construction shows us that organism and environment are not distinct physical objects; they become fitted to each other as co-evolving dyads.[61] The gene-centric account is insufficient in this respect because it recognizes this co-evolution of organism and environment only to the extent that genes can be invoked. As

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[58] Oxygenic photosynthesis is the process of converting solar energy to a metabolically accessible form, while generating oxygen as a byproduct.

[59] Dates of the Great Oxidation Event are still debated, although the general consensus is that oxygen began to build up in Earth's atmosphere – as a result of the photosynthetic activity of cyanobacteria – about 2.5 billion years ago.

[60] The presence of an organism includes all of its living activities, such as energy acquisition by means of photosynthesis. Later in Chapter 4 I will argue that we can understanding photosynthesis in terms of Merleau-Ponty's idea of *comportment*— the way organisms carry out or carry forth their existence.

[61] Robert (2003) uses this term "co-evolving dyad" in *Embryology, Epigenesis, and Evolution*.

we saw in Dawkins' theory of the Extended Phenotype, environmental features such as beaver lakes gain evolutionary significance because they can (and in principle, *should*) be traced back to genes "for" the beaver's behaviour.[62] The same phenomenon receives another interpretation under NCT. The effects of a beaver's dam are not the product of genes as extended phenotypes, but operate at the level of organisms and ecology.[63] As Wells puts it, "While niche construction theory locates animal artefacts in their constructors' environment, hence treating them as capable of exerting selective pressure on both the constructors and their descendants, the extended phenotype concept assimilates artefacts with their constructors' genes" (Wells, 2015, 547). We can further show the distinction between Dawkins' idea of the extended phenotype and NCT with the case of endoparasite[64] influencing their hosts' behaviour, for example, between parasitic flukes and snails. When snails are infested by flukes of the *Leucochloridium* genus, their behaviour changes from light-avoiding to light-seeking, which brings them to places that are more conspicuous to bird, the next host for the fluke to complete its life cycle.[65] Dawkins here would interpret light-seeking behaviour of the snail as the extended phenotype of fluke genes, i.e. within the fluke are genes for snail behaviour. In this example, we arrive at a somewhat confusing situation of distributing phenotypes between organisms, it is unclear to which organism we should attribute the genes "for" light seeking-behaviour. In a sense, light-seeking behaviour is a phenotype of the snail (albeit as an infected snail), snail), but *also* the extended phenotype of the

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[62] As I have already quoted in Chapter 1, "If beaver lakes could fossilize, we would presumably see a trend towards increased lake size if we arranged the fossils in chronological order. The increase in size was doubtless an adaptation produced by natural selection, in which case we have to infer that the evolutionary trend came about by allele replacement. In the terms of the extended phenotype, alleles for larger lakes replaced alleles for smaller lakes." (*The Extended Phenotype*, 233)

[63] If Dawkins goes so far as to include beaver lakes as part of their extended phenotype, it is unclear why he stops here, rather than extending the effect of their genes to the whole wetland ecosystem in which beavers are keystone species.

[64] Parasites that reside within the body of their hosts.

[65] Flukes also live within the retractable "horns" of a snail, the same place that is photosensitive. The horns of an infested snail further resemble maggots that trick birds into eating them.

parasitic fluke according to Dawkins. Since light-seeking behaviour is detrimental for the snail but beneficial for the fluke,

> *if* this is to be regarded as a parasitic adaptation… we are forced to postulate the sometime existence of *genes* in the parasite gene-pool that influenced the behaviour of hosts, since all Darwinian adaptations evolved by the selection of genes. By definition such genes were genes 'for' snail behaviour, and the snail behaviour has to be regarded as part of the phenotypic expression of fluke genes. (*Extended Phenotype*, 213, emphasis mine)

Representing gene-centrism, what Dawkins takes for granted in this account is the fact that *organisms* first exist as the condition of possibility for the evolution of parasites. In favour of a niche-construction interpretation of endoparasites, Wells (2015) argues that

> despite Dawkins' view that it is possible to 'emancipate' phenotypes entirely from organisms, organisms appear to be central to the endoparasitic story. Not only do organisms account for the existence of parasites in the first place…the disposition of parasite and host bodies seems to make possible the phenomenon at issue, namely the existence of parasite genes for host behaviour.

For Wells and NCT, animal artefacts such as beaver dams, or endoparasites that change their hosts' behaviour are phenomena best understood in terms of a niche-constructing organism shaping their environment, rather than in terms of genes and extended-phenotypes.

To pick up on something that Wells suggested in his criticism of Dawkins, I would like to add that an "adaptive" parasite is not one that immediately kills its host, but co-evolves with its host to continue its own persistence. This is also true for examples of disease and viruses; as a disease or parasite *co-evolves* with their host, the result is that they tend to become more contagious and mild, rather than immediate and deadly.[66] What I think is lost in Dawkins' and the gene-centric accounts is the essential role of organisms as the key explanatory component of

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[66] This is why *novel* strains of a virus (e.g. swine flu) tend to be more dangerous than established ones (the common cold). If a virus is both contagious and deadly, before long it would deplete its host population to one that is no longer viable for the virus. Hence, over time, parasites, diseases, or viruses tend to evolve to be more mild, co-adapted to the deference of the host in such a way that optimizes the extent to which they can be contagious, rather than dangerous.

parasitism. It is the particular biology (physiology, morphology, behaviours, etc.) of the snail that make possible different interactions with the fluke, parasitism being one instance. Because gene-centrism does not begin from the level at which these interactions take place (which is at the level of organisms and ecology), we come to problematize both organisms (by reducing them to genes) and the environment (by distinguishing it from organisms as a distinct entity). In my view, these obstacles encourage a reconsideration of the premises and commitments of modern evolutionary theory. From EED and NCT we see that the mechanistic account is not a basis from which we can cover sufficient grounds; plasticity, inter-organism relations, and much of ecology are left unaccounted for. To acknowledge the role of organisms in a positive manner can both facilitate our investigation of phenomena such as plasticity, and allow further insight into examples such as parasitism. In the following section I hope to add to the significance of plasticity by showing how it can be interpreted as a mode of niche construction.

2.3 Plasticity as a mode of niche construction

Borrowing from Sonia Sultan, in this section I would like to reintroduce developmental plasticity as *experiential niche construction*.[67] While Sultan considers organism experiences as a mode of niche construction to show its adaptive relevance, my considerations will differ in that experience is central for what I want to argue. From the fact that organism have experiences, I will argue for my own view that organisms are "meaningfully involved" with their context of existence. What I want to show here is that biologists are already aware of the relevance of organism experiences for evolution. Going beyond this in later chapters, I will argue that it is with a phenomenological account that we can further clarify the significance of experiences and meaning; more specifically, it is from an account of the organism as a *lived-body* that we can draw the connection between plasticity and experience, including the adaptive value of their connection.

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[67] Sultan argue for this view in her book *Organisms* and *Environment* (2015).

The idea that plasticity is a mode of niche construction follows from the fact that adjustments to an organism's biology mediate an organism's *experiences* of the physical environment. To clarify, what I mean by "experience" is that organisms are involved with their environment *perceptually* or *perspectivally*, to the capacity of what is open to their senses.[68] For example, a bird that catches sight of a butterfly has an "experience" of the butterfly, with a perception that extends to the UV spectrum that is invisible for humans. Similarly, I would also say that trees have an "experience" of sunlight given the photoreceptive qualities of their leaves. Even without changing their physical conditions of existence, by changing their own morphology, physiology, and behaviours, organisms can inhabit the same surrounding conditions in a different, more favourable manner, and it is through their worlds of experience that organisms live and adapt.[69] Sultan writes,

> Largely through phenotypic plasticity and other ecological developmental adjustments, individual organisms not only respond to the environments they encounter, they change the encounter itself, in many cases to one more favourable for their own function. (Sultan, 41-42) …Adaptation is not the playing out of a selectively scripted encounter between an internally determined phenotype and an impervious external environment. (Sultan, 74)

We can distinguish between two modes of niche construction depending on the manner in which organisms construct their niche. On the one hand, there is niche construction as it is typically understood: organisms construct, especially through certain behaviours, a niche or habitat by changing conditions of the physical environment. Niche construction as such can be clarified as *habitat construction*, where "habitat" refers to features of the physical world that organisms modify by means of their behaviours. In general, examples of habitat construction tend to focus on organisms that are motile and "behave" in its usual meaning associated with animals,

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[68] It is with the connection to perception and perspective that I will introduce an account of the lived-body. Also, what I mean by "sense" here is very general, organism experiences are founded through their senses, and via their senses, organisms take on a manner by which things show up.

[69] In Chapter 3, I will refer to this "lived" environment by Uexküll's formation of the *umwelt*.

the beavers dam or ant hills are paradigm examples of niche construction presented in this manner. In another sense, niche construction can be achieved through developmental plasticity, when organism alter themselves and in turn their own *experiences* of the physical environment. Again from Sultan,

> An equally universals aspect of niche construction is the way that an individual's realized phenotype—including its morphology, physiology, and behavior in a given environment—shapes and transforms how the individual *experiences* that environment, apart from any measurable effects on the external parameters. (Sultan, 41, emphasis mine)

Experiential niche construction is important for showing us the limitations of gene-centrism, because nowhere in the gene-centric account does it speak of the experiences of organisms, or how these experiences contribute to the course of their evolution. For examples of experiential niche construction, plant life most readily reveal its significance, since the capacity for having experiences does not require motility or a standard conception of "behaviour" (limited to animals) as its pre-condition.[70] Given that plants are sessile organisms, they lack the motility of a foraging animal with the option of *relocation* if resources become scarce, or if they are in the presence of their herbivores or competitors. However, as Sultan notes, what plants have in place is "an impressive developmental repertoire that can serve to enhance their *experience* of the below—and above—ground resource conditions they encounter as sessile organisms."[71] Plasticity can be realized in all parts of a plant—from their root systems, overall structure, leaf morphology, and floral arrangements—plants are developmentally plastic in ways that optimize their experiences of environmental conditions in their favour, or at least minimize the experience of conditions that are unfavourable.[72] For example, through the plasticity of their root systems, plants can meet their

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[70] In Chapter 4, I will argue that the concept of "behaviour", especially when we speak of plant examples, adopts a more general sense as *comportment*, which can include developmental plasticity as one of the way in which organisms comport themselves.

[71] (Sultan, *Organism and Environment*, 80, emphasis mine).

[72] What is "favourable" or "unfavourable" depend on the biology of the plant. For example, acid soil is favourable to blueberries, but unfavourable to asparagus which grows better in slightly alkaline soil.

nutrient requirements without physically moving to another location. In their experience of soil nutrients, plants can modify their roots by changing their root surface area to volume ratio,[73] with targeted growth and increased rate of nutrient uptake at nutrient-rich microsites.[74] In this way, many plants are able to maintain a consistent experience of resources, even if the physical environment itself is limited and patchy (and this is often the case).

For another example, we can observe adaptive leaf plasticity in the plant *Polygonum persicaria.* Just as animals are able to orient their bodies for thermoregulation,[75] plants can realize the same effects by plastic changes in their morphology.[76] Using genetically identical clones, clones that are grown in shade conditions will produce thin and broad "shade leaves", whereas clones that are grown in light conditions have thick and narrow "sun leaves". Since light conditions naturally coincide with an increase in heat, thick and narrow leaves minimize water loss from the leaf surface (which happens inevitably through transpiration and evaporation). Conversely, broad and thin leaves have increased surface area for photosynthesis, catching more energy to compensate for the lack of available light in the physical environment itself. By changing their morphology, leaf plasticity allows *P. persicaria* to both optimize its experience of light in shade conditions, as well as minimize its experience of heat in light conditions.[77]

What makes this example more interesting is that *P. persicaria* is also an invasive alien species. While they are native to Eurasia, *P. persicaria* became invasive after its introduction to North America. In their "natural", evolutionary-historical context, native (rather than alien)

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[73] Increase in surface area without drastically changing volume means that a plant can be more efficient in seeking out soil nutrients, without increasing its biomass which requires additional growth.

[74] See (Hodge, 2009) and (Hutchings and de Kroon, 1994).

[75] For example, Texas horned lizards contribute to their thermoregulation by taking on a stance that elevate their bodies further away from the ground (heated desert sand). Desert snakes also have certain patterns of locomotion to minimize their contact with the desert sand.

[76] Sultan describes this in much more detail than I have alluded to. Not only is leaf morphology plastic, the overall structure of the plant, down to the cellular constitution of a leaf are modified. For details see (Sultan, *Organism and Evolution,* 81).

[77] For more details on these experiments see (Sultan & Bazzaz. 1993a, 1993b).

species co-evolve with their environment along with biotic and abiotic ecological factors, such as predators, that keep their populations in check. When introduced to a novel environment, without certain ecological relations in place, some organisms then become invasive when introduced as alien species; which is to say, there is no such thing as an invasive species *per se*, what is “invasive” only makes sense with reference to an ecological context. Given that the “ability to succeed in diverse conditions is a key factor allowing introduced species to successfully invade and spread across new areas,”[78] plasticity plays a significant role in the possibility of species becoming invasive. We can see the role of plasticity in the invasive capacity of *Polygonum cespitosum* (a close relative of *P. persicaria*) in more detail. Research shows that for invasive populations of *P. cespitosum*, individuals are more plastic than native populations of the same species. Through plastic changes to their physiology and morphology, invasive populations of *P. cespitosum* can accommodate a greater variety of ecological conditions than their native counterparts.[79] This accommodation is possible because plastic organisms can maintain a consistent *experience* of the conditions necessary for their persistence, even if they are foreign to the environment of their introduction.

Conclusion 2

Contrary to the mechanistic view, these examples suggest key limitations in the view that organisms are machines reducible to their genetic constitution. Plasticity—here as experiential niche construction—shows us that organisms are not only irreducible to genes (and in the other

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[78] (Matesanz *et al.*, 2012).

[79] “We also compared the introduced-range populations to a single population from the native Asian range, and found that the native population had delayed phenology, limited functional plasticity, and lower fitness in both experimental environments compared with the introduced-range populations.” (Sultan & Matesanz, 2015). Also from (Matesanz *et al.*, 2012), “Our results indicate that the future spread of *P. cespitosum* in its introduced range will likely be fueled by populations consisting of individuals able to express high fitness across diverse light and moisture conditions, rather than by the evolution of locally specialized populations.”

direction, organisms cannot be constructed from their genes); the *experiences* of organisms, as a function of their plasticity, matter for the trajectory of their evolution. Organisms are also not removed from the environment as distinct physical objects. Regarding the organism-environment relation by which adaptations take place, we should recognize that

> biologically **meaningful** environments are not separable from organisms; organisms do not simply confront preexisting environmental scenarios. Rather, by virtue of their expressed phenotypes, organisms themselves shape or "construct" (1) the *external* conditions of their existence [habitat construction], and (2) their *experience* of those external conditions [experiential niche construction]. As a result of these two modes of *niche construction*, individual organisms play an active role in their own adaptation by shaping the very selective conditions that contribute to present fitness and subsequent evolution. (*Organism and Environment*, 37, my emphasis in bold)

This idea of the biologically *meaningful* environment will be a central point of focus in the chapters that follow. Going beyond objections within biology, from Uexküll's *Umwelt Theory* (Chapter 3), I will address how the environment can become meaningful for organisms via his articulation of the "functional/meaning cycle". The examples of plasticity I discuss in this chapter will also show the limitations of Uexküll's theory, leading to a phenomenological interpretation of organisms that I develop in Chapter 4. If indeed plasticity can be interpreted as "experiential niche construction", and plasticity operates at the level of the organism body, I will further examine the way in which organism experiences (as a capacity of perception) cohere with the organism body. In Chapter 4, I will argue that it is from Merleau-Ponty that we can draw this connection.

Chapter 3 —Uexküll and the subjective worlds (umwelten) of animals

In this chapter I present a second criticism of mechanistic biology developed by Jakob von Uexküll, with supplementary ideas from his son Thure von Uexküll; I will refer to Jacob von Uexküll simply as Uexküll, and Thure von Uexküll as Thure. Both Uexkülls are 19–20th century German biologists and founding figures of *biosemiotics*—the combined study of biology and semiotics, the study of life with the study of signs and meaning. While Uexküll precedes the *Modern Synthesis*, his criticisms are nonetheless applicable to mechanistic biology as I understand it. For my interests, Uexküll's *Umwelt Theory* provides a more explicit departure from mechanism compared to objections within contemporary biology.[80]

I will first outline Uexküll's biology as a continuation of the Kantian worldview (Section 3.1).[81] I will argue that Uexküll's Umwelt Theory goes against the two commitments of mechanism I described in Chapter 1, which is for the project of biology to reduce organisms to their physical constituents, and assimilate organisms and the environment in terms of physical objects. Uexküll instead moves biology "within" the organism-subject by a Kantian turn. It is this move to the "subjects" of biology that I take as an allusion to a phenomenology interpretation of organisms, namely, Uexküll's thesis that organisms have experiential worlds, which he calls their *umwelten* (Section 3.2). However, I say that Uexküll's account is only an allusion to a phenomenological interpretation because a strict adherence to Uexküll commitments remains insufficient for what I wish to argue. Insofar as Uexküll posits a complete and perfect fitting of organisms to their umwelten (Section 3.3),[82] his Umwelt Theory is incapable of realizing adaptive

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[80] Namely, what I discussed in Chapter 2 (ecological evolutionary development and niche construction theory).

[81] More specifically, Uexküll's biology uses the *Critique of Pure Reason* rather than Kant's more explicit account of biology from the *Critique of Judgement*.

[82] This is Uexküll's first / fundamental principle of Umwelt Theory. I will discuss this point in more detail later in this chapter.

change, and phenomena such as developmental plasticity are again overlooked as they were under a mechanistic framework (Section 3.4). For both Uexküll and mechanists, it is problematic that adaptive plasticity is left out of biological theory as a remainder still to be explained. Furthermore, by considering plant examples, I will argue that Uexküll does not in fact draw out the full implications of introducing meaning to biology. Although I think Uexküll's account is phenomenological in some of its gestures (precisely, his attention to meaning), I will later argue that it will instead be the efforts of Merleau-Ponty that allow a proper framework to account for the manner in which organisms meaningfully relate with their umwelten.

3.1 Uexküll's two tasks of biology

For Uexküll, what characterizes mechanism is the belief in the existence of natural laws that are independent of human conception or existence (TB, xiv). What motivates mechanism and what it aims to achieve is scientific realism, whereby our scientific theories are directed at an objective world that exists in and of itself. Uexküll criticizes that scientific pursuits as such situate themselves only on an act of *faith* rather than reason. Instead of following the mechanistic framework already accepted for the physical sciences, biology should explore, in two directions, the achievements of Kantian philosophy. For Uexküll, the project of biology should expand Kant's thesis that the world owes its appearance to subjective forms of intuition (e.g. time, space, causality), and any science that aims to get "beyond" the phenomenal realm is mistaken about the scope of its own research. Uexküll writes,

> No attempt to discover the reality behind the world of appearance, i.e. by neglecting the subject, has ever come to anything, because the subject plays the decisive role in construction the world of appearance, and on the far side of that world there is no world at all. *All reality is subjective appearance*. This must constitute the great, fundamental admission even of biology. (TB, xv)

Uexküll then describes his own project as an "endeavour to reproduce in current biological terminology the main results of Kant's line of research" (TB, xv). On the one hand, biology should elaborate on how the unique worlds of organisms—i.e. their umwelten—are subjectively constituted "by considering the part played by the body, and especially by our sense-organs and central nervous system" (TB, xv). Uexküll writes,

> Only when we have clearly understood the problem of the sense organs will the manner in which the whole organism is built become clear. At the outer boundary, they serve as a gutter for the physicochemical effects of the outside world. (TM, 48)

On the other hand, biological research should examine "the relations of *other* subjects, animals, to objects" (TB, xv), biology should expand the Kantian worldview from human experience and apply it to other organisms.[83] I will refer to Uexküll's first task of biology as a question about the body of organisms, or how different organic bodies figure into their subjective phenomenal worlds (umwelten). Addressing this first question will establish a partial solution to Uexküll's second task, which I interpret as a question about other organisms and organism-environment relations.

3.2 Umwelt Theory: participatory observation and the meaning cycle

What allows Uexküll to make claim to the umwelten of other (organism-)subjects is by a method of *participatory observation*.[84] Since umwelten are constituted by their subjects through biological signs, Uexküll's method of participatory observation is the way in which we can investigate the *meaning* of these signs (Thure, 1982, 3). "Observation" begins by examining one's own sensory organs and proceeds to the sense organs of other organisms, as Thure describes,

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[83] This is also the order in which Uexküll presents the two tasks of his biological project.

[84] I take this description from Thure von Uexküll; Jakob von Uexküll does not himself refer to his method of umwelt-research as "participatory observation".

> Observation means first of all ascertaining which of those signs registered by the observer [the umwelt-researcher] in their own experiential world are also received by the living being under observation. This requires a careful analysis of the sensory organs (receptors) of the organism in question. After this is accomplished, it is possible to observe how the organism proceeds to decode the signs it has received. (Thure, 1982, 4)

While observation is the attempt to identify the role of an organism's sensory organs and sense receptors that establish the range of an organism's world of experiences (FWM, 166), to "participate" is to reconstruct an organism's umwelt from the results of observation defined above.

> Participation, therefore, signifies the reconstruction of the Umwelt of another organism, or—after having ascertained the signs which the organism can receive as well as the codes it uses to interpret them—the sharing of the decoding processes which occur during its behavioral activities. (Thure, 1982, 4)

Although umwelt-research necessarily begins from the limits of our own experience as researchers, it is nevertheless legitimate because sense organs and receptors are proper to organisms themselves. The method of participatory observation should not be confused with an act of sympathy or empathy,[85] because it does not claim to give us firsthand experience what it is like to be another organism, or live their umwelten. Instead, it always aims to describe their umwelt by an organism's own sense capacities, even though we do not have direct access to the precise content of their umwelt.

In his *Foray into the Worlds of Animals and Men*, Uexküll uses the method of participatory observation to make a case for the existence of other umwelten. Beginning with the Tick as his example, Uexküll shows us how each—and by universal instantiation—*every* umwelt is constituted by the interplay of perception and action, between the world of perception (world-as-sensed, *Merkwelt*) and world of action (*Wirkwelt*). This interplay Uexküll refers to as the *functional* or *meaning cycle* (Figure 2).[86]

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[85] Sympathy and empathy are also ways by which we can relate to the experiences of other subjects; participatory observation aims to distinguish itself from this kind of relation.

[86] Figure retrieved from (TM, 32).

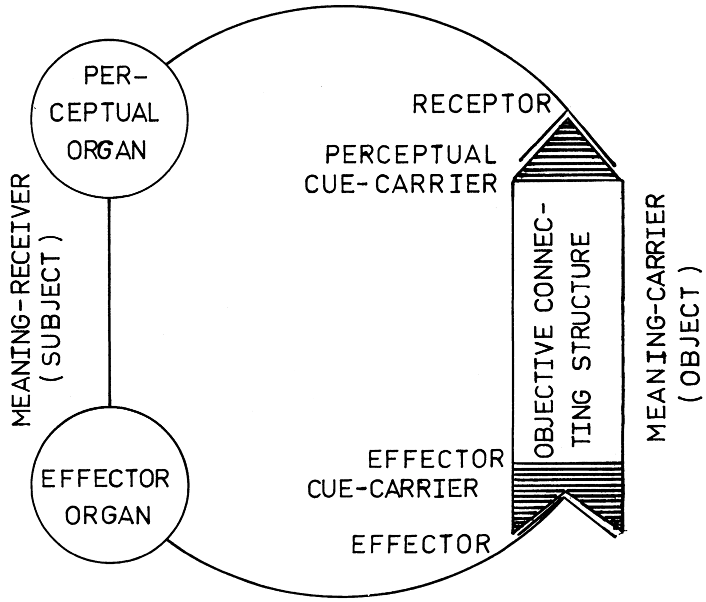

Figure 2. Uexküll's *functional* or *meaning cycle.*

It is via the meaning cycle that perception links to action, and organism-subjects to objects. Thure describes the meaning cycle in the following manner,

> If we run through the various phases of [participatory observation], we come upon the model [and method] for the [study] of other [organisms] constructed by Jakob von Uexküll—the *functional circle*. In this, the subject (as 'self') embraces the object like a forceps with its two claws: on one hand as *receiver* (receptor) [here referring to the world of perception], which receives stimuli and transposes them into signs, thus structuring the 'nonself' with perceptual cues (properties of an object); on the other hand as *operator* (effector) [here referring to the world of action], which changes or erases the perceptual cues or properties of the 'nonself' with operational cues. (Thure, 1982, 18-19, emphasis mine)

By contrast to the machine-mereology of mechanistic biology—where organisms and the environment are distinct objects that relate in a causal manner—umwelt-research concerns their relation of *meaning.*[87] In his *Theory of Meaning*, Uexküll shows us how a single environment of the meadow can vary considerably between different organisms and their respective umwelten.

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[87] Or the phenomenological idea of *intentionality*.

Between a flower-picking girl, an ant, a spittle-bug (froghopper) larvae, and a cow, the same flower stem will appear to each subject under different tones of meaning, as ornament for the girl, path for the ant, faucet for the larvae, and food for the cow. The same flower stem shows up via different signs and functional *tones*, depending on the subject to which it appears. For another example, the same oak tree that mechanists hold to be objective and independent of organisms will instead take on different meaningful tones depending on whether it appears to a forester, fox, owl, squirrel, ant, beetle, or ichneumon wasp. Uexküll writes,

> In accordance with the different effect tones, the perception images of the numerous inhabitants of the oak are configured differently. Each [umwelt] cuts out of the oak a certain piece, the characteristics of which are suited to form the perception-mark carriers as well as the effect-mark carriers of their functional cycles. …In the hundred different [umwelten] of its inhabitants, the oak plays an ever-changing role as object… If one wanted to summarize all the different characteristics shown by the oak as an object, this would only give rise to chaos. Yet these are only parts of a subject that is solidly put together in itself, which carries and shelters all [umwelten]. (FWM, 130 and 132)

From these examples of the flower and oak tree, Uexküll concludes that "there are thus purely subjective realities [i.e. umwelten] in [objective] environments.[88] But the objective realities of the surroundings [i.e. the physical environment of mechanistic biology] never appear as such in the [umwelten]" (FWM, 125). To mechanistic biology, Uexküll's example of the meadow flower would appear only as a meaningless object, as "a tangle of ether waves and air vibrations, of finely distributed clouds of chemical substances and mechanical contacts which have their effect from object to object". (FWM, 163). From Umwelt Theory, there is not one universal, objective "environment" shared between different organisms; different organism-subjects suggest an equal

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[88] Uexküll also gives examples of organisms meaningfully relating to non-living, inanimate objects. For example, "The stone, which lies as a relationless, neutral object in the hand of the [indifferent] observer [i.e. the mechanistic biologist], becomes a carrier of meaning as soon as it enters into a relationship with a subject. Since no animal ever plays the role of an [indifferent] observer, one may assert that no animal ever enters into a relationship with an "object" [that is, as soon as an animal relates to an "object", it is no longer an "object" *in itself*, but becomes something *for* the animal subject]. Through every relationship the neutral object is transformed into a carrier of a meaning that is impressed upon it by a subject." Combined translations from (FWM, 140) and (TM, 27-28).

number of different umwelten within the same physical environment (FWM, 42). Within the same physical conditions, there exist a plurality of meaningful worlds that are unique to each organism.[89] This directly goes against the basic assumptions of mechanism that is committed to the constancy of (mind-independent) objects;[90] Uexküll's Umwelt Theory supports only a *constancy of subjects*. Again by contrast to the commitment of mechanism to an "objective" environment, Uexküll writes,

> No single property of matter remains constant as we course through the series of umwelts. Each object observed by us changes not only its meaning tone but also the structure of all of its properties, in form as well as content, from umwelt to umwelt… [T]he constancy of matter on which the [mechanists] insist is no solid basis for an encompassing worldview. Much better founded than the constancy of objects is the constancy of subjects (FWM, 197-198).

The concept of scientific "objectivity", our commitment to the reality of objects, is itself one of the ways in which things *appear* within our human umwelt. As Uexküll tries to show us, what gets neglected from the mechanistic theory is precisely our own (human) perceptual domain of experience, what appears in an "objective" manner always involves a transformation

> into perception marks or perception images and equipped with an effect tone, which *only then* makes them into real objects, even though no part of the effect tone is present in the stimuli… [T]he simple functional cycle teaches us that perception marks as well as effect marks are expressions of *the subject* and that the qualities of the objects included in the functional cycle can only be referred to as their vehicles. (FWM, 125, emphasis mine)

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[89] Following a Kantian way of thinking about (subjective) umwelten and the (objective) environment, for Uexküll to say that umwelten are "appearances" does not diminish their reality. Like Kant, Uexküll maintains that there exists a natural world *in-itself* (the Kantian noumenon), the content of which is wholly inaccessible to us except through our subjective forms of intuition (the Kantian phenomenon). While the "objective" environment (as Nature in-itself) furnishes organisms with their umwelten, the only thing we can say about it is that it exists. Mechanistic biology is improper in that it goes too far in making realistic assumptions as if it had access to Nature in-itself.

[90] Again, the specific version of mechanism that Uexküll has in mind is characterized by a commitment to realism.

Between subjective experiences “internal” to organisms, and “external” objects in the world, there is always a *cycle of interpretation* between organisms and the world as it appears—this is why Uexküll’s functional cycle is also a meaning cycle. If biology in general concerns the relation between organisms and their umwelten, and it is by relations of meaning that organisms engage with their conditions of existence, then the question of meaning in biology ought to take priority over causal processes—which can only make sense *after* investigations of meaning (FWM, 151). We can articulate the central thesis of Uexküll’s Umwelt Theory as such,

> Meaning is the pole star by which biology must orient itself, not the impoverished rules of causality which can only see one step in front or behind, antecedents and consequents to which the great connections, interrelations, and interactions remain completely hidden. (FWM, 160)[91]

It is with Uexküll’s attention to meaning that I will later turn to a phenomenological interpretation of organisms. Here going further than Niche Construction Theory (NCT), Uexküll shows us that meaning and organism experiences are facts from which we should *begin* biological research. While NCT also acknowledges the contributions of organism experiences for biology, it does so only to the extent of emphasizing its adaptive significance. For Uexküll, it is not enough to merely highlight *adaptive* instances where the experiences of organisms are relevant, the very task of biology is to investigate the experiential worlds of organisms. Also going further than NCT, Uexküll gives an account of *how* the environment can become meaningful for organisms—viz. by the cycle of perception and action between the organism-subject and objects in the world.

3.3 The melodic interpretation of organisms and their perfect and complete umwelten

The distinction Uexküll introduces to contrast the mechanistic interpretation is the melodic interpretation of organisms. For Uexküll, organisms should be understood by analogy to music,

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[91] Combined translation from (TM, 43).

where the parts of organisms cohere like notes (cells) and melodies (organs) of a symphony (the organism).[92] Ecologically, the relation between organisms and their context of existence (including interactions with other organisms) are understood as duets and harmonies. For example, between bees and flowers, Uexküll notes that bees can perceive in the ultraviolet spectrum of light, what this implies is that

> the yellow color of a flower on which a bee lands, we can say with certainty that the flower is not yellow in the bee's [umwelt]… because the color spectrum of the bee's eye has a different scale of lightwaves than does the color spectrum of our eye.… No single property of matter remains constant as we course through the series of environments. Each object observed by us changes not only its meaning tone but also the structure of all of its properties, in form as well as content, from environment to environment. (FWM, 197)

Contemporary biology both confirms and continues to study this example of bees. Between bees and flowers, bee-pollinated flowers often have patterns called "nectar guides" that are only visible to us by UV photography, revealing an UV absorbing center and UV reflecting periphery. While bees can themselves perceive in the UV spectrum, it is only with the help of modern technology that humans can represent the flower as it appears to its pollinators. Many studies show that flowers with nectar guides have both greater pollinator visitations and better pollinator orientation.[93] For contemporary evolutionary biology, such a relation between flower appearance and the perceptual capacity of its pollinators are understood as *co-adaptations*. As I mentioned in Chapter 2, the Extended Synthesis (particularly from Niche Construction Theory) also emphasized co-adaptations in terms of organisms and their ecological context becoming fitted to

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[92] See (TM, 51-52), Uexküll writes, "The process by which the subject is progressively differentiated from cell-quality, through the melody of an organ to the symphony of the organism, stands in direct contrast to all mechanical processes, which consist of the action of one object upon another. …The effect of the meaning-factors of plants and of the meaning-carriers of animals on their meaning-utilizers demonstrates this point very clearly. As the two parts of a duet must be composed in harmony—note for note, point for point—so in nature the meaning-factors are related contrapuntally to the meaning-utilizers. The shaping of the form of living beings will be more understandable only when we have succeeded in deriving a theory of the composition of nature from it."

[93] See (Primack, 1987) and (Papiorek *et al*., 2016).

each other as co-evolving dyads.[94] For Uexküll, this relation is understood by analogy to music, it reflects the ongoing duet or harmony between organisms and their umwelten. What gets described as "fitness" within a scientific framework is for Uexküll natural "*counterpoints*".[95] By Uexküll's framework, ecological dynamics describe the fitting together of point and counterpoint, motif and motive (FWM, 190).

> The color of the flowers is not the same for the bees as for us, but it serves the bees nonetheless as a certain perception feature, since the flower and the bee are composed *contrapuntally* and in *counterpoint* to each other. (FWM 187, italics mine)
>
> Were the flower not beelike,
> And were the bee not flowerlike,
> The consonance could never work.[96]
> (FWM, 190)

For Uexküll, between bees and flowers there is a "bee-likeness" of the flower and "flower-likeness" of the bee. It is their likeness to each other that organisms and the environment appear (and cohere) in such a way that contemporary biology interprets by a concept of fitness. Here I take Uexküll's explanation of fitness as the point at which his theory differs most with mainstream evolutionary theory. For scientific biology, fitness—the appearance of adaptedness between organisms and their surroundings—is understood as an *achievement* over time, rather than the condition from which organisms begin. Organisms evolve *towards* a likeness with their surroundings via natural selection (when individuals that are better able to survive and reproduce in an environment persist over others that are less able).[97] Conversely for Uexküll, the phenomenon of fitness reflects the harmonious composition of nature, it shows us that

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[94] See the examples of the Great Oxidation Event and of invasive species discussed in Section 2.1.

[95] Again following the analogy to music.

[96] Here Uexküll is following Goethe's saying: "*Were the eye not sunlike, It could never gaze upon the sun. Were the sun not eyelike, It could not shine in any sky*" (FWM 190) – this is itself a comment on Plotinus' theory of vision in the *Enneads*.

[97] In short, this is the Darwinian theory of selection or "survival of the fittest" where fitness is precisely defined as a measure of those that persist.

> the two voices [of the organism and environment] have to be composed for each other note for note, point for point, meaning factors in Nature stand in contrapuntal relation to the meaning utilizers [organisms].
> (FWM, 171)

> At least to me, no imperfection was apparent even in the simplest animals. As far as I could judge, the material available for construction was always used in the best possible way. Every animal had its own life stage, populated with all the things and all the fellow players that were meaningful for its life. The-characteristics of the animal and those of its fellow players harmonized everywhere with assurance, like the points and counterpoints of a many-voiced chorus: It was as if the same masterful hand were gliding across the keys of life since time immemorial. One composition followed the other, endlessly many, serious and light, majestic and terrible. (FWM, 195)

In my reading, the relation that Uexküll draws between organisms and their surroundings is one that *presupposes* and takes for granted the relation of fitness. Uexküll therefore situates his account of biology past the point at which fitness is something that requires further explanation. Conversely for Darwinian theory and scientific biology, fitness is something that must be explained as one of the most basic phenomena of evolutionary biology, and it is the explanation of "natural selection" that covers both the phenomenon of fitness and organic diversity. According to Uexküll, Darwinian theory reaches a limit because it neglects biological meaning and subjectivity.[98] Darwinian biology "suppresses" the fact that organisms meaningfully constitute their environments-proper (i.e. umwelten). When Darwin explains the apparent unity of organism-environment relations in terms of "survival of the fittest",[99] this contributes nothing to understanding the characteristics of organisms (notably, their umwelt formation) that give them their status as living, systematic, and meaningful entities. At the same time, for Uexküll to presuppose the coherence between organisms and their surroundings is to deny the problem (which Darwin articulates) of a "struggle of existence". Umwelt Theory denies the "struggle for

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[98] This is true given the "state" and development of Darwinian theory at the time Uexküll was writing.

[99] This is for Uexküll only an accidental conglomeration of traits that somehow come together under physical conditions that allow the persistence of individuals with those traits.

existence" as a proper description of ecological interactions,[100] even if we take it as an ecological fact, the "struggle for existence" is inessential to biology which should instead focus on signs and meaning. While Uexküll is aware that not every interaction is consonant for individual organism,[101] nevertheless, he contends that there is always an overall unity for the species, to focus on the "struggle for existence" misses the bigger picture that is the grand orchestra of Nature.

Indeed, the supposed fitness of organisms in relation to their umwelten was already implied by Uexküll's meaning cycle; it was by considering the meaning cycle that Uexküll first arrived at the founding principle of his Umwelt Theory, he writes,

> The connection of subject to object can be most clearly explained by the schema of the functional cycle. The schema shows how subject and object are interconnected with each other and form an orderly, systematic whole. If one further imagines that subjects are linked to the same object or different ones by multiple functional cycles, one can thereby gain insight into the fundamental principle of [Umwelt Theory]: *All animal subjects, from the simplest to the most complex, are fitted into their [umwelten] with equal perfection or completeness*. (FWM, 49-50, emphasis mine)[102]

Herein lies my contention with Uexküll's Umwelt Theory. While I think Uexküll is correct to say that different organisms respectively fit into their umwelten with equal completeness—such that we should not understand one organism to be better adapted to its umwelt than another organism to their umwelt—I disagree with Uexküll's *presupposition* of fitness. To posit a perfect and complete fitting of organisms and their umwelten is to have a static theory of life that denies

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[100] "Proper" in the sense of being a pre-theoretical description that is not already theory laden.

[101] Look for Uexküll's discussion of "the sufferance of meaning" in (FWM, 182-185); Uexküll writes, "The meaningful role for the spider's web in the life of the fly is in no way in the fly's interest — in fact, it contradicts it. The fly, entangled in the web, cannot use this meaning-carrier in its Umwelt at all: it can only tolerate [suffer] it.… The significance of these apparent contradictions of meaning is immediately clarified when we disregard the particular individual and consider only the species as a whole."

[102] Combined translation from (Uexküll, *Stroll*, 324).

organic evolution. Even if we bracket the issue at the level of ecology,[103] at the level of individual organisms, Uexküll cannot account for phenomena such as plasticity of development; Uexküll's theory is therefore insufficient to explain facts of life that are unique and characteristic of life. Given that plasticity is a fact about organism bodies, it is at the point of embodiment that I aim to show shortcomings of Uexküll's theory in more detail (Chapter 4). In the following section I will elaborate on this point of plasticity as a fact about organism bodies, and my aim is to show that plasticity can both challenge and contribute to Uexküll's umwelt-research, specifically his own task of biology to study the role of organism bodies in umwelt formation.[104]

3.4 Organism bodies: animals, plants, and plasticity

3.4.1 Maintaining functional cycles by developmental plasticity

What I want to show in this section is that organism bodies are problematic for Uexküll's theory given the fact of developmental plasticity. At the level of individual organisms, plasticity challenges the fundamental principle of Umwelt Theory which posits a perfect and complete, i.e. rigid organization between organisms and their umwelten. Instead, I will argue that the appearance of fitness is made possible by plasticity, as an achievement of the body rather than condition to take for granted. Going further than Uexküll's efforts to re-establish a place for organisms in biology, developmental plasticity shows us that organisms are even more active in contributing to their umwelten than Uexküll allowed for, meaning cycles are actively *maintained* via plasticity of the body.[105] To include plasticity therefore expands Uexküll's theory beyond the

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[103] For example, the issue of changing organisms and changing physical environments, which we know is the case through the fossil record and geology.

[104] I will continue these arguments about the body in Chapter 4, borrowing from Merleau-Ponty's account that relates the body to perception.

[105] And not just any body (as *Körper*), but a body actively lived by the organism (as *Leib*). In the next chapter I elaborate on what it means for organisms to be lived-bodies.

formal fact that organisms simply have umwelten, it allows us to elaborate on the details of how umwelten are mediated by their organism-subjects.

To support my point with an example, in the *Aurelia* moon-jellyfish, specifically in their ephyra life-stage,[106] experiments show that when there is damage to their radial body structure, individuals *reconfigure* their bodies to achieve their typical radial form without *regenerating* any new parts, even though *Aurelia* are known to be capable of regenerating from a single tentacle (Abrahms *et al*., 2015). The breakdown and repair of an organism's body structure can reveal what is basic about their bauplan; to have reconfiguration over regeneration is to have plasticity of the bauplan itself. Rather than regenerating their bodies, reconfiguration suggests that a *general* structure suffices (and perhaps is even preferable for rapid repair) in place of having a more *precise* body form, in this example, being radially symmetric suffices for the *Aurelia* without necessarily having tentacles in groups of four.[107] For free-swimming jellyfish, the significance of maintaining a radially symmetric body is its contributions to locomotion and feeding. Ephyrae and medusae move by means of *propulsion*, contracting and expanding their bodies to take in and force out water, and propelling themselves in the opposite direction. When moving by propulsion, jellyfish also receive feed-back about their own body structure, since propulsion is intrinsic for both sensing and repairing their body symmetry (*Abrahms et al*., 2015). Without radial symmetry, propulsion becomes inefficient to impossible.[108] Radial symmetry is further important for free-swimming jellyfish because of their mode of feeding. When food sources are suspended

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[106] "Jellyfish", which are technically *Cnidarians*, exhibit "alternation of generations" between their free-swimming *medusa* form and their sedentary *polyp* form. Polyps strobilate to *asexually* produce *ephyrae*, which mature to become medusae, while medusae *sexually* reproduce gametes, the union of which grow to become a polyp. Thus it takes two (re)productive cycles for each medusa or polyp to have offspring that resembles itself.

[107] All cnidarians follow a bauplan that is radially symmetric in groups of four (dissectible to equal parts along two horizontal axes), this is true for both their sedentary polyp phase and free-swimming medusa phase.

[108] Given the way jet-propulsion works, we can imagine that asymmetric jellyfish might rotate or flip in the water rather than propelling themselves in a direction.

in water, finding food often depends on opportunities of encounter; radial symmetry allows the jellyfish to perceive all around itself and therefore increase the chances of feeding.[109] To be more considerate, I would like to speak of propulsion as a general life-activity of free-swimming jellyfish, rather than to distinguish different activities of feeding, locomotion, even respiration and excretion (for which propulsion also plays a role, but I will not discuss them in addition to locomotion and feeding). While feeding obviously differs from respiration, jellyfish do not have distinguished systems for these activities, there is no respiratory system or proper digestive system, these life activities are unified in propulsion.[110]

Uexküll also uses the jellyfish as an example to illustrate the "simple" functional cycle (Foray, 74-76). The medusa, as an example of a "reflex animal", has only *one* functional cycle from the rhythmic contractions of its body, which creates an ongoing cycle between its own effect mark and perceptual mark (Foray, 75). Given the significance of radial symmetry for all aspects of the jellyfish life style, damage to radial symmetry would significantly affect their functional cycles; the asymmetric jellyfish is disoriented from its usual world of perception (to perceive all around) and world of action (propulsion). Both the perceptual and effective world—the two forceps constituting Uexküll's functional cycle—fundamentally depend on the jellyfish's body structure. Indeed, Uexküll himself recognized an important connection between the organism body and their meaning cycle, he writes,

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[109] By contrast to finding *situated* food sources for terrestrial organisms. This is also different for the sedentary polyp form, chance encounters (enhanced by radial symmetry) can be more important for feeding given their infrequent locomotion; although they can still move by summersaults. Note that in the history of animal evolution, the capacity for more direct locomotion coincides with having a bilateral bauplan.

[110] Uexküll was also aware of the unity of jellyfish activities (Uexküll, *Foray*, 75). For the sake of argument I have simplified the jellyfish to make a case, a better example of unified life-activities is the sponge (technically: the porifera). Sponges are sessile "filter-feeders", filtering is not only how sponges feed, but also how they respire, excrete waste, and reproduce / exchange gametes. Jellyfish at least have an internal body cavity and tissue level of organization with hints of a "digestive system".

> Once we are finally convinced by an overwhelming number of examples that each Umwelt is at base filled only with meaningful symbols, then a second, even more astonishing fact forces itself upon us: *Each subject's symbol is at the same time a meaningful theme for the structure of the subject's body*. The body that houses the subject on the one hand produces the symbols that populate the surrounding garden and is, on the other hand, the product of these very same symbols that are the meaningful themes in constructing it. (TM, 77)

In what follows I will elaborate on Uexküll's conception of the organism body and why his exclusion of plant bodies makes his account inadequate. For now, what I want to emphasize is the role of the body that *maintains* an organism's meaning cycle—this Uexküll did not acknowledge in drawing the connection between the body and meaning. Plasticity of the body is essential for achieving a general body structure, the success of which results in a meaningful and coherent umwelt for the organism. The second point I want to make with this example is that if we examine the umwelt of an organism, what we need to explore and articulate is the relation between perception and embodiment—this I will take up again in the next chapter by introducing Merleau-Ponty's account of the lived-body.

3.4.2 Animal versus plant bodies in Uexküll's Umwelt Theory

In his clarification of the conditions for organisms having umwelten, Uexküll draws a distinction between animal and plant bodies. Only animals properly have umwelten because they have both perceptual and effector organs, along with the ability of locomotion. By contrast, plants lack perceptual organs and locomotion, and without perception they cannot have meaning cycles in a way that is properly instantiated by animals. In my view, Uexküll's exclusion of plants from having proper umwelten marks an important limitation in his theory, from this insufficiency I suggest that we should reconsider the conditions for having an umwelt. With some examples I hope to show that plants have both a world of action and a world of perception, albeit without having "organs" of perception or exhibit locomotion *per se*. I will argue that plants also meet the conditions for having umwelten, like animals, plants also have perceptual and effect worlds, and form meaning cycles with the physical environment.

First to be clear, Uexküll is often inconsistent about whether or not plants have umwelten, or at least meet the conditions for having umwelten. As such, I will focus on his account of the *differences* between plants and animals, given that animals decidedly have umwelten. At times it seems that Uexküll supports at least a very basic umwelten of plants, he says,[111]

> For plants, too, there are vitally important stimuli that set themselves apart as *meaning factors* from the effects which press in upon the plants from all sides. The plant encounters these external effects not with the help of receptor or effector organs but, rather, it is *capable of making a selection of stimuli* from its dwelling-shell thanks to a living layer of cells. (FWM 147, emphasis mine)

The ability of plants to have meaning—to mediate and "choose" from physical stimuli, seem to suggest that plants, at least in a basic way, have subjective-worlds that are distinguished from their physical conditions of existence. However, and for the most part, Uexküll explicitly denies that plants have umwelten, because umwelten depend on having both perceptual and effective worlds, he writes, "There are certainly no nerves or sense organs in plants, so that their whole existence seems to play itself out in an effect world." (FWM, 162). If plants exist only in the effect world without a world of perception, they cannot properly constitute a meaning cycle and umwelten.

For Uexküll, there are two points at which plants differ from animals such that they lack a world of perception: their bodies and their comportment.[112] The body of the plant remains within the effect world because it lacks proper *sense organs* of perception, Uexküll writes,

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[111] Elsewhere he also says, "The dwelling-world [i.e. umwelt] of an animal, which we see spread out all around it, transforms itself when observed by the animal subject into the latter's environment…The dwelling-world of a plant, which we can demarcate around its location, transforms itself, observed from the standpoint of the subject "plant" into a dwelling-shell that is composed of various meaning factors subject to regular changes. The vital task of animal and plant consists in utilizing the carriers of meaning or meaning factors, respectively, according to their subjective structural plans." (FWM, 150)

[112] I will discuss the idea of comportment much more in Chapter 4.

> Animals as well as plants build themselves living houses in their bodies with the help of which they carry on their existence. …The guide-rope of each functional cycle, insofar as it runs through the animal's body is the nervous system, which, beginning with receptors (sense organs), guides the current go stimulation through the central perception and effect organs to effectors. The plant's house does without the nervous system; it lacks the perception and effect organs. *As a consequence, there are no carriers of meaning for the plant, no functional cycles, and no effect marks.* The animal's house is mobile and can move its receptors anywhere with the help of its muscles. *The plant's house does without its own [mobility]; since it possesses neither receptor [perceptual organs] nor effector organs with which it could construct and control its environment. The plant possesses no special environment organs but is immediately immersed in its dwelling world.* (FWM, 146-147, emphasis mine)

Reading the above passage, I think it is unclear and problematic why umwelten exist only for animals with perception and action *organs*,[113] moreover, it is further problematic why *motility* is required for having umwelten. If we observe the activities (not yet to say their "behaviour") of plants and others sessile organisms, I think they attest to having phenomenal worlds, and specific world of perception which Uexküll rejects in plants. Even without appealing to more obvious examples of motility, such as flower heads following the sun or *Mimosa* leaves responding to touch, if we examine the diversity of leaf morphology and leaf arrangements (phyllotaxis) between different plants around the world, botanical examples strongly suggest that plants *experience*[114] their surroundings. As an example, if we look at a desert cactus, with its photosynthetic stems and leaves modified into spines, or a rainforest arum, with its broad waxy leaves and drip-tip, both plants seem to mediate the physical condition of heat. The dry heat of the desert is mediated by the cactus having virtually no leaves (which would increase body temperature by exposing more surface area to the desert sun), and instead performs photosynthesis on part of its water storing stems (the body of the cactus). In turn, for the humid

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[113] Here "organ" means a specific part of the body that performs a certain function (as distinguishable by anatomical studies); organs arise by a functional differentiation within the more general framework of an organism's "life activities"

[114] Here I mean "experience" in a specific sense of the term: experience entails meaning, for plants to "experience" their surroundings is for plants to mediate their conditions of existence.

heat of the rainforest, an arum plant has waxy leaves that both prevent evaporation and repel water, and a drip-tip to keep off the rain. Contrary to Uexküll's account of plants, neither the cactus nor the arum seem to be "immediately immersed" to the desert or rainforest. If perceptual and effect marks are the conditions of possibility for mediation and meaning, given that plants mediate their conditions of existence, we can infer that plants also have perceptual and effect marks by which they, like animals, "interpret" their conditions of existence without being abandoned to it.

Recall that Uexküll's first task of biology is to consider how the phenomenal worlds of organisms are constituted "by considering the part played by our body, and especially by our sense-organs and central nervous system" (TB, xv). This question should be pursued by his method of "participatory observation", when we determine the biological signs and meanings of other organisms by first examining our own systems of signs, and then reconstructing the umwelten of other organisms such that we can "participate" in them. The account of body which accompanies Uexküll's umwelt-research and method of participatory observation is the body as a "living house" or "dwelling-shell". What is important about organic bodies is that they "house" the nervous (neurosensory)[115] system which establishes the scope of an organism's meaning cycle. Contrary to Uexküll's attachment to the nervous system, with the previous example of the *Aurelia* jellyfish, I have tried to show that it is instead the body structure of an organism that is essential to their meaning cycles. Although I agree with Uexküll that details of the neurosensory system contribute to meaning cycles, in my view, this should not imply the stronger claim that neurosensory systems alone set the requirement for what it is to constitute a meaning cycle. It is problematic for me that Uexküll does not speak of sensory systems in general, but only the neurosensory systems of animals. A more inclusive understanding of "sensation" would consider examples such as plants "sensing" the direction of sunlight, even though we would not attribute

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[115] Senses elaborated from and connected to a nervous system.

any neurosensory system or perceptual organs to the plant. It seems that the sense in which Uexküll is interested in a question of the body is really an interest in the question of animal neurosensory systems, with an understanding of perception as a mode of consciousness. Since Uexküll distinguishes between different bodied organisms, he places himself below the level at which embodiment *in general* is relevant for umwelt-research. When describing his first task of biology, Uexküll has already delimited his umwelt-research within the domain of zoology.

As a fact of organism bodies, I have tried to show that plasticity is problematic for Uexküll. Given that organisms are almost always developmentally plastic, and given the adaptive significance of plasticity, there is no perfect or complete fitting of organisms to their umwelten. Here I should like to add that plant examples most readily show plasticity and its biological significance; as such, plants are especially problematic for Uexküll's Umwelt Theory. In my view, Uexküll's limit of umwelt formation to animals forgets the initial clue that lead him to develop Umwelt Theory in the first place, namely, the awareness that organisms are subjects because they have phenomenal worlds which they constitute. According to Uexküll, plants lack perceptual worlds and exist only in the world of action (FWM,162), plant worlds are limited to the plant's physical location because they lack motility (FWM, 147); in general, plants lack meaning cycles and the capacity of meaning-formation that animals readily exemplify. Real examples contest against these claims. For examples, many species of Bamboo have synchronized gregarious flowering, when individuals of the same cohort flower together regardless of where they grow around the world. In the species *Phyllostachys bambusoides*, individuals growing in different parts of the world flower together every 130 years (the longest recorded interval between flowering). Using Uexküll's vocabulary, Bamboo seem to have their own specific meaning cycles, which they uphold notwithstanding differences between individual physical conditions and locations of existence. If indeed plants were "abandoned" to their physical locations, there would be no such thing as synchronized flowering.

Even when flowering is "triggered" by physical conditions, this possibility requires that plants be *receptive* of their physical surroundings, i.e. have a world of receptivity or world of perception. Botanists refer to the capacity of plants to vary their flowering according to light exposure as photoperiodism (Chamovitz, 2013). "Long-day" plants such as Irises or Barley require more exposure to light in order to flower, and "short-day" plants such as Chrysanthemums and soybeans flower with less exposure to light.[116] While it seems that photoperiodism support's Uexküll's claim that plants are "immediately immersed" in their locations, the possibility of this immersion—to observe that plants respond to physical cues—requires that plants have a kind of "perception" in the first place. As such, I would like to suggest that plants and sessile organisms in general have phenomenal worlds, the requirement of locomotion is too strict as the condition for having meaning cycles or the capacity of meaning-formation. In the next chapter I propose a more general concept of movement that includes bodily plasticity as an instance (viz. *motricity* of the lived-body), to be plastic suffices for having different umwelten without the organism physically relocating.[117]

Conclusion 3

In this chapter I have tried to explain Uexküll's objections against mechanistic biology from his Umwelt Theory. For Uexküll, biology proper ought to take a Kantian turn to the *subjects* of biology, and study the way in which animals constitute their subjective worlds by means of their world of perception and world of action. Uexküll's Umwelt Theory offers us

> an answer to the central question of biology about the relation of living organisms to the surrounding world: Living systems are not related to

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[116] Photoperiodism is how we can artificially manipulate plants to flower around holidays, e.g. chrysanthemums around Mother's Day.

[117] I think if physical relocation is required for having different umwelten, this requirement weakens one of the key claims of Umwelt Theory: stability of organism-subjects over objects.

> their Umwelt by causes and effects in a causal mechanical way, but connected by *signs* that have *meaning* for them. (Thure, *Eye Witness*, 347)

What I want to bring forward to the next chapter is the transition from scientific biology to a focus on organism experiences and meaning. While I value Uexküll's promotion of meaning for biology, I disagree with his hypothesis of perfect and complete organism-environment relations that do not allow for evolution, and I further disagree with his limitation of umwelt-formation to zoology. In the next chapter I will try to show that plants, too, unambiguously have umwelten, and they do so by means of the plasticity of their bodies. What I identify as centrally problematic in Uexküll is his conception of the organism body as a "dwelling-shell", in the next chapter I will argue that we should instead interpret the organism body from Merleau-Ponty's idea of the *lived-body*. Lastly, I will argue that insofar as Uexküll maintains the subject-object (in-itself, for-itself) dichotomy inherent in Kantian philosophy, he does not in fact give an adequate account of the meaningful involvement between organisms and their umwelten.

Chapter 4 - Phenomenological interpretation of organisms

In Chapter 2, I criticized the mechanistic interpretation of organisms using objections within scientific biology. From Ecological Evolutionary Development and Niche Construction theory, we honed in on a key limitation of the mechanistic interpretation as it cannot account for the phenomenon of developmental plasticity and its adaptive value therein, including its contribution in shaping organisms' *experiences* of its environment in a favourable manner. In Chapter 3, Uexküll showed us a more radical turn against mechanism as he began his project of biology on the basis of biological meaning. Contrary to the mechanistic—which is for Uexküll, metaphysically realistic—commitment to the constancy of objects, Uexküll instead argued for the constancy of organism-subjects, which he further took as evidence for rejecting Darwinian evolution in favour of the perfect and complete fitting of organisms with their umwelten. Both the subjective world of Uexküll's "umwelten" and environmental "niche" from a scientific understanding already gesture to the idea that organisms are *meaningfully involved* with their context of existence; indeed, the mechanistic account itself appeals to a role of biological meaning in a tacit manner. My goal now is to develop an interpretation of organisms with an explicit emphasis on their meaningful involvement. Given that phenomenology is a project to return to and learn from phenomena what we eclipse (both elude and cover over by the same act) in analytic thought, what I purport to show is that by taking a phenomenological consideration of organisms: we can both (1) better make sense of certain phenomena from which theories of previous chapters find support, and further (2) make up for some of their limitations. These two points will guide the phenomenological interpretation I develop in this chapter. Lastly, by giving a phenomenological interpretation of organisms, what I hope to show is the interrogatory potential of a phenomenological analysis beyond the standard considerations of philosophy of biology.

What I explore is an account that retrieves the meaningful involvement of organisms via an interpretation of them as *lived-bodies*.[118] I will draw on Merleau-Ponty's account of the lived-body, organism comportment, and the activity-passivity relation to show how we can (1) elaborate on the particular manner of their meaningful involvement, without at the same time committing to vitalistic commitments, and (2) overcome the problem posed by developmental plasticity (especially of plant life) for the adequacy of mechanistic biology and Uexküll. I will first criticize mechanistic biology from a phenomenological point of view (Section 4.1). In order to show how organisms are meaningfully involved with the environment, I will argue that we require a particular kind of dynamism and feedback associated with Merleau-Ponty's idea of the lived-body. The kind of feedback that belongs to the live-body was only partially articulated by Uexküll in terms of the meaning cycle (Section 4.2), in addition, I will argue that meaningful involvement requires that we consider organism-environment relations not in terms of the alternation between pure activity and passivity (Section 4.3).[119] As I will argue, organisms are neither passively abandoned to the physical environment (as products of environmental selective forces), nor is the environment a product of organism activities that create or constitute the environment anew.[120]

4.1 Phenomenological critique of mechanistic biology

While my task is to criticize mechanistic biology from a phenomenological point of view, we should recognize that the mechanistic interpretation also depends on the "phenomenon" of

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[118] Neither mechanism nor Uexküll can adequately capture the organism body as such. While mechanism focused only on the "objective" aspect of the body, Uexküll went too far on the side of "subjectivity", to the point where organisms superimposed a second order of reality (a Kantian phenomenal world distinguished from things in-themselves) within which they lived their lives.

[119] More specifically, the ideas of passivity and activity should not be understood antithetically, both gets at one side of the passivity-activity structure.

[120] Here I mean a very positive sense of activity that would exclude phenomena such as photosynthesis as an organic "activity".

organisms.[121] Given the way in which organisms *appear*—and it is in this sense that I mean the "phenomenon" of organisms—organisms themselves present us with the preliminary evidence for a mechanistic interpretation. Moreover, organisms must *first* appear,[122] and only by appearing can we *then* try to understand them conceptually; i.e. the mechanistic interpretation, as an instance of conceptual understanding, depends on the way in which organisms initially show themselves. To acknowledge here that organisms are the phenomenal basis of the mechanistic interpretation does not, however, further imply that we agree with the direction mechanism takes us. Rather, the role of a phenomenological interpretation is to *retrieve* the phenomenon of organisms from its mechanistic distortion. By bracketing mechanistic commitments and giving reinterpretations of the same phenomena, I will argue that a phenomenological approach can do better than mechanism as it explicitly orients us to focus on meaning in biology.

To reiterate, what I criticized as the "mechanistic" interpretation of organisms is predicated on two assumptions: (1) the possible reduction of organisms to genes, and (2) machine-mereology that construes organisms as if they are *partes extra partes*. From these commitments I tried to show that gene-centrism is the point of arrival for a mechanistic interpretation, which is inadequate because it excludes organism experiences and their meaningful involvement for evolution. While the elision of meaning is itself a problem for the mechanistic interpretation, given that mechanism also derives its evidence from the phenomenon of organisms, it is doubly problematic that mechanism does not recognize when it in fact tacitly appeals to the idea of meaning (which it otherwise denounces by its own standards). To put it simply, what mechanism denies, yet depends on for its explanations, is biological meaning. The mechanistic interpretation

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[121] We do not undermine the reality of organisms by calling it a phenomenon in this case, because phenomenon here is distinguished from "mere appearance", or something concealing the real and true manner in which organisms exist. For phenomenology, the phenomenon of organisms *is* the organism in-itself.

[122] This is why Merleau-Ponty gives primacy to perception in his discussion of consciousness. Perception is the means by which anything *can* appear to us in the first place, and accordingly, the preliminary way in which we can be conscious (of).

must therefore go beyond itself in order to make up for its exclusion of meaning,[123] whereas a phenomenological interpretation allows for meaning in its very set up.[124] If we examine ideas in the Modern Synthesis such as evolutionary *neutrality*, biological *cues* (e.g. as triggers for gene-expression), or organism *solutions* to environmental *problems*, I suggest that these concepts already require us to evoke an idea of meaning.

- *Evolutionary neutrality*: to distinguish between variations of evolutionary change, the Neutral Theory of Molecular Evolution introduced "neutral" molecular changes that contrast the "directed" changes by natural or sexual selection.[125] Evolutionary change as such can be explained purely in terms of molecular changes to the genome, changes that are neither beneficial (adaptive) nor deleterious (maladaptive), but negligible to the overall fitness (survival and reproduction) of an organism. What I want to suggest here is that an idea of meaning is already at work in discussing evolutionary neutrality. In order for molecular changes to be neutral, they depend on the manner in which an organism is, and is *already*, involved in an ecological context. If we consider *adaptive* relations between an organism and its environment (relations to which "neutral" changes are defined by contrast), I suggest that adaptation is an instance of an organism's meaningful involvement more generally. This is because what it means for an organism to be adapted to its environment is for certain qualities of the environmental to be biologically significant and "have meaning" for the organism. If there are neutral evolutionary changes by contrast to adaptive ones, neutrality should also be defined contextually. For example, and here I adopt the Modern Synthesis

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[123] As I will soon argue in more detail, in our attempt to go beyond mechanistic biology, its exclusion of meaning leads the way for the *vitalistic* interpretation of organisms. However, vitalism also distorts the phenomenon of organisms by taking the implications of biological meaning too far.

[124] This I have tried to show in the Introduction. Phenomenology investigates (the realm of what has) meaning

[125] Evolutionary biologists speak of different "directions" of selection, which can be stabilizing, divergent, or disruptive.

narrative: for water striders that live on the surface of a pond, “adaptive” genes include those that code for phenotypes that help them stay afloat by mediating water surface tension, such as genes for bodies and postures that evenly distribute their body weight. By contrast, “neutral” changes to a water strider’s genome are changes that do not affect their ability to mediate water surface tension. We can restate the Modern Synthesis narrative here to say that surface tension is something *meaningful* for water striders, which sets up the criteria for genetic changes to be adaptive or neutral in the first place. The idea of biological meaning provides the context in which anything *can* change adaptively or neutrally, without it, mechanism itself (machine mereology and reductionism) is inadequate to articulate a sense of evolutionary neutrality.

- *Organism solutions to environmental problems*: Along the same lines of argument as above, I think there is already an appeal to meaning in the adaptationist narrative of organism “solutions” to pre-existing environmental “problems”. From the previous example, if we say that water surface tension poses a *problem* for water striders to stay afloat and alive, and they in turn *resolve* this problem through their genetically determined morphology and behaviours—this is likewise to say that the phenotype of water striders (the organism solution) addresses the surface tension of water (environment problem) in a relation of meaning. By contrast, if we say that water surface tension does *not* pose an adaptive problem for dolphins, this is because surface tension is not a meaningful factor given the way in which they dolphins engage with the same physical environmental conditions (body of water). In general, I think there would be no such thing as a pre-existing environmental “problem” and subsequent organism “solution”, if they did not (already) mutually address each other through a relation of meaning.

- *Biological cues*: As Uexküll already tried to show us, the fact that anything *can* be a biological cue requires that it is "interpreted" by organisms through their function/meaning cycles. For example, butyric acid is a "cue" for ticks because it is shows up to them as a sign or indicator of the presence of their host (mammals). The possibility of biological cues depend on animals being meaning-giving and meaning-bearing subjects; the physical environment itself does not present any "cues" without animals that incorporate them in their world of experience. Within an organism's umwelt, objects of the physical environment *become* cues by taking on a meaningful tone in which they show up for an organism,[126] in this way, when mechanistic biology speaks of environmental cues for an organism (e.g. environmental cues that trigger gene-expression), it already presupposed relations of meaning as a condition.

From these examples what I want to suggest is that it is given the context of an organism's meaningful involvement with the environment that many important ideas of the mechanistic account obtain their content. Taking a phenomenological consideration, we can further say that mechanism exceeds itself *because* it is based on the phenomenon of organisms; mechanism inevitably encounters biological meaning in its concepts even when it tries to rule meaning out. To the extent that mechanism utilizes the idea of meaning, we can say that it only anticipates meaning without further drawing its biological implications.[127] As such, I will argue that phenomenology can do better than mechanism because it allows us to investigate meaning explicitly as our focal point.

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[126] For Uexküll, what we understand as the physical environment is itself limited to our human umwelten and scientific construction; and following Kant, the world in-itself or the noumenal world is wholly inaccessible except for the fact that it exists.

[127] Conversely, vitalism takes the implications of meaning too far.

4.1.1 Merleau-Ponty's criticisms of mechanistic behaviour

In *The Structure of Behavior* (SB),[128] Merleau-Ponty examines the subject-object distinction by analyzing the phenomenon of behaviour as a neutral starting point with respect to what is in-itself (objective Nature) and for-itself (subjective consciousness).[129] By examining behaviour, and later, the phenomenon of perception, his goal is to undo our long held distinction between pure subjectivity and pure objectivity, and in turn establish a "*for-us*, *in-itself*" or "*in-itself, for-us*" (PhP, 74). Here I would like to extend Merleau-Ponty's criticisms of the mechanistic interpretation of behaviour to the mechanistic interpretation of organisms more generally. Just as mechanism cannot give us a sufficient account of behaviour, I will argue that we cannot sufficiently understand the adaptive appearance of organisms from mechanistic principles. In order for Merleau-Ponty's arguments to follow through, my characterization of mechanistic biology in Chapter 1 was already set up on the basis of his treatment of mechanistic behaviour. I would also like to open up Merleau-Ponty's use of *comportment* (which he used to speak of animal behaviour) to a broader understanding that includes developmental plasticity as an instance.[130] This is to say, I consider organism development as part of the way in which they carry out (comport) their existence. By extending the idea of comportment to include plasticity, drawing on phenomenological sources, my goal is to further clarify the adaptive value of plasticity beyond its

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[128] While the original French title is *La structure du comportement*, the focus of the book is on animal behaviour rather than "comportment" in general as I take it to mean.

[129] For Merleau-Ponty, the phenomenon of behaviour is neutral with respect to its "physiological" (objective) and "mental" (subjective) interpretations. (SB, 4). In *Phenomenology of Perception*, he continues to investigate the subject-object distinction in terms of intellectualist and empiricist interpretations of perception. In general, what he means by *subjective* includes consciousness, Kantian idealism, intellectualism, what is *for-itself* (*pour-soi*); and by *objective* includes the idea of Nature, scientific realism, empiricism, and what is *in-itself* (*en-soi*).

[130] Rather than an idea of comportment with the emphasis on behaviour, as if there is no more to comportment than behaviour (which I think is the case for Uexküll).

articulation in eco-evo-devo and niche construction theory, and with this, further raise it as an objection against mechanism and Uexküll.[131]

For Merleau-Ponty, the mechanistic interpretation of behaviour is marked by (1) "*realistic analysis*" that decomposes animal behaviour into isolable elements *partes extra partes*, and from these parts, we can pre-determine the total set of behaviours available to an organism by the combination and recombination of behavioural elements (e.g. stimuli and response).[132] The mechanistic account of behaviour also depends on (2) causal explanations that appeal to physical laws by which the elements of behaviour are secondarily reconnected.[133] Looking at animal behaviour in its basic instance as reflex behaviour, the mechanistic interpretation decomposes behaviour it in terms of environmental stimuli, places of excitation, reflex circuits, and the organism's reaction (SB, 10-33). Behaviour understood as such depends on the possibility of assigning, mapping, and reducing organism reactions to nerve functions and nerve topography. Behaviour gets reduced to its "place of excitation" that depends on the overall static anatomy of an organism, and the organism is further taken to be passive because it is limited "to executing what is prescribed for it by the place of the excitation and the nerve circuits which originate there." (SB, 9) Modelled on the physical sciences, mechanism establishes as its very condition of intelligibility a world of physical objects assembled by causal laws. The mechanistic account of behaviour

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[131] Later I also attempt to explicate the adaptive value of plasticity it in terms of the connection between the lived-body and perception.

[132] Merleau-Ponty writes, "In the classical conception…[to] explain nerve functioning can only be to reduce the complex to the simple, to discover the constant elements of which behavior is constituted. Thus one would decompose the stimulus as well as the reaction until one encountered the "elementary processes" composed of a stimulus and a response which were always associated in experience. …In principle, to each part of the stimulus there should correspond a part of the reaction. And the same elementary sequences, combined differently, should constitute all the reflexes." (SB, 11)

[133] "The classical theory of the reflex and the methods of realistic analysis of causal explanation, of which the reflex theory is only an application, alone seem capable of constituting an objective and scientific [i.e. mechanistic] representation of behavior. The object of science is defined by the mutual exteriority of parts and processes." (SB, 9)

therefore leads to the elision of meaning because it admits biological reality only at the physical level.[134] Merleau-Ponty tells us,

> The incompleteness of lawful [i.e. mechanistic] knowledge does not oblige [mechanism] to grant [any other] mode of knowledge because the uncoordinated residue [viz. biological meaning] does not lend itself to any verifiable determination, except perhaps those which science will obtain later by the invention of new laws. The law remains therefore the model of *all* truth. (SB, 155, emphasis mine)[135]

From mechanistic beginnings, meaning does not show up as a biological truth because it cannot be investigated mechanistically by way of realistic analysis. What this means for the scientific study of animal behaviour is that

> one must reject every notion of intention or utility or value [i.e. meaning] as subjective because they have no foundation in [objective] things and are not intrinsic determinations of them. If I am hungry and, absorbed in my work, I extend my hand toward a piece of fruit placed near me by chance and lift it to my mouth, the piece of fruit does not act as an object invested with a certain *value*; what releases my motor reaction is an ensemble of colours and lights, a physical and chemical stimulus [of wavelengths of energy]. …If behavior *seems* intentional [and meaningful], it is because it is regulated by certain *pre-established* nerve pathways in such a way that in fact I obtain satisfaction. (SB, 9, emphasis mine)

Even if mechanistic biologists allow something *like* meaning in biology, mechanism operates under the assumption that meaning is a mere appearance given the pre-established correspondence between environmental stimuli and organism response. Explaining the adaptive value of behaviour amounts to finding predefined nerve pathways (viz. reflex circuits) through

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[134] In this sense, Merleau-Ponty's account of mechanism is similar to that of Uexküll, both characterize mechanism by its commitment to scientific realism.

[135] By "lawful knowledge", what Merleau-Ponty is referring to are the mechanical laws of physics.

which stimuli cause organisms to react in terms of reflexes.[136] Merleau-Ponty raises his objection here that mechanism is mistaken about the nature of its incongruence with meaning. The difficulty with meaning is not a fact of organic complexity at the physical level, a problem that mechanism can overcome by attending to more causal details of the physical organism. Rather, the meaningful comportment of organisms is something that mechanism cannot account for *in principle*, thereby leaving it as a remainder that cannot be factored into mechanistic solutions, and for which vitalism—as the theoretical antithesis to mechanism—must secondarily attempt to supplement (SB, 3).[137] Indeed, Merleau-Ponty argues that both mechanism and vitalism begin from the realistic analysis of organisms, with the common assumption that

> the organism [is] considered as a segment of matter, as an assemblage of real parts juxtaposed in space and which exist outside of each other, as a sum of physical and chemical actions. All the events which unfold in this organism possess the same degree of reality [in terms of its status as a physical object]. (SB, 151)

While mechanism keeps itself within the domain of physical objects, what vitalism adds to the realistic account of organisms is its own distortion of meaning as something extra-physical, irreducibly over and above the organism body (e.g. an entelechy supervening the physical body). For Merleau-Ponty, the fact that mechanism leaves biological meaning unaccounted for makes it susceptible to these objections from vitalism. From mechanistic beginnings we lapse into vitalism because vitalism is required to counter the realistic, physicalist limitations of mechanism. In this

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[136] "If the order in the reflex—that is, the adaption of the response to the stimulus and the coordination of partial movements in the total gesture—is assured by pre-established connections from the sensible surface to the effector muscles, the classical conception puts considerations of topography in a position of primary importance; the place of the excitation should decide the reaction; the stimulus should act by those of its properties which can modify the anatomical elements taken one by one; the nerve circuit should be isolated since the reflex, if it were not guided in this manner, could not be adapted to the stimulus as it is in fact." (SB, 10)

[137] In setting up the project of his book, Merleau-Ponty writes, "The situation is not the same in biology. In fact the discussions concerning mechanism and vitalism remain open. The reason for this is probably that analysis of the physico-mathematical type progresses very slowly in this area and, consequently, that our picture of the organism is still for the most part that of a material mass *partes extra partes*. Under these conditions biological thought most frequently remains realistic, either by juxtaposing separated mechanisms or by subordinating them to an entelechy." (SB, 3)

way, both mechanism and vitalism share a common distinction between matter and meaning, both begin from the organism as a material entity to which meaning must be introduced at a later time.

> [A]s long as one views behaviour as a mundane event, interpolated between antecedent and subsequent events and really contained in a sector of space and a segment of time, …life (and consciousness) will be introduced as the additional conditions which supplement the inadequate physical determinants. (SB, 133)

Contrary to both sides of the mechanism-vitalism antithesis, Merleau-Ponty argues that

> [t]he object of biology is to grasp that which makes a living being a living being, that is, not—according to the *realist* postulate common to both mechanism and vitalism—the superposition of elementary reflexes or the intervention of a "vital force," but an indecomposable *structure of behavior*. (SB, 46, emphasis mine)

Instead of explaining behaviour from the realistic analysis of organisms, Merleau-Ponty proposes that it is in terms of a dialectical, gestalt *structure* that we can come to terms with how (as the manner in which) animal behaviour is meaningful. By examining the "structure" of behaviour, we find a way out of the mechanism-vitalism antithesis that dominates traditional discussions of organisms. In what follows I will extend Merleau-Ponty's account of the structure of (animal) behaviour to speak of organism comportments in general, particularly against the mechanistic interpretation of organisms shown by gene-centrism.

4.1.2 Merleau-Ponty's *gestalt* interpretation of behaviour

In my own account of mechanistic biology, Merleau-Ponty's idea of realistic analysis includes both aspects of machine mereology and reductionism. Adopting his term, I suggest that the Modern Synthesis and gene-centrism employ realistic analysis in their interpretation of organism appearance—in terms of "phenotypes" (of which behaviour is an instance) that are reducible to genes and gene-expression. In the Modern Synthesis, realistic analysis further gives an absolute status to the environment as something that imposes selection pressures upon organisms, and it does this without considering how the environment is presented (or how the environment is able to presents itself) to the organism in the first place.[138] Contrary to the realistic analysis of organisms, Merleau-Ponty argues that it is instead by an *existential analysis* of the organism that we come to understand how the environment "matters" for an organism. In other words, our account of behaviour should include an effort to discover the lived-meaning of behaviour, and given the way in which organisms *actually* exist, rather than the abstractions of mechanism when it tries to understand the organism in a part-by-part, "objective" manner.[139] Merleau-Ponty clarifies that

> In recognizing that behavior has a meaning and depends upon the vital significance of situations, biological science is prohibited from conceiving of it as a thing in-itself (*en soi*) which would exist, *partes extra partes*, *in* the nervous system or *in* the body; rather it sees in behavior an embodied dialectic which radiates over a milieu immanent to it. (SB, 161, emphasis original)

It is in a dialectical gestalt structure that the meaning of behaviour makes its appearance. To break this down, Merleau-Ponty speaks of the *gestalt structure* of behaviour because the figure-ground (viz. gestalt) relation marks the manner in which the meaning of behaviour comes to the fore. Moreover, it is in terms of the organism-environment *dialectic* that we can express how meaning is exhibited. Taking on a dialectical relation, organisms address themselves to their environment through relations of meaning. Merleau-Ponty tells us,

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[138] Applying realistic analysis, we forget and forgo an organism's meaningful involvement with the world—involvement that organisms already live as the factual condition for the mechanistic interpretation. Realistic (reflective) analysis does the same for the phenomenon of perception. Merleau-Ponty writes, "the presumptive signification of the object [i.e. what is deemed "objective"] without wondering how it enters into our experience. Reflective analysis replaces the absolute existence of the object with the thought about an absolute object, and, by attempting to view the object from above or by attempting to conceive of the object from [everywhere and] nowhere, reflective analysis destroys the object's internal [viz. perspectival] structure." (PhP, 211, emphasis mine).

[139] To clarify, the *actual* way in which organisms exist includes what is virtual to them (e.g. taking up a goal, having a phenomenal world), to deny this by a strictly "realistic" account of organisms is an abstraction.

> The relations of the organic individual and its milieu are truly dialectical relations…and this dialectic brings about the appearance of new relations which cannot be compared to those of a physical system and its entourage or even understood when the organism is reduced to the image which anatomy and the physical sciences give of it. Even its elementary reactions cannot be classified, as we have said, according to their apparatuses in which they are realized, but according to their vital significance. (SB, 148-149)

Taking on a dialectical structure, the organism-environment relation is an "emergent" phenomenon in the sense that it is irreducible to either qualities of the organism or qualities of the environment.[140] What we need, therefore, contrary to reductionism and machine-mereology, is an *organic* mereology whereby (1) the organism as a whole is not reducible to its parts, and (2) in relation to their environment, organisms are entangled via their meaningful involvement, as opposed to being distinct physical objects; the kind of organic mereology we are after depends on the organism as a lived-body (Section 4.2.1).[141] For now, what I want to show are the criticisms of reductionism and machine mereology from Merleau-Ponty's gestalt interpretation of behaviour.

> In a form [gestalt], the whole is not the sum of its parts. Even if one accepts the fact that the organism is accessible to a physical analysis which is unlimited in principle…it is absolutely certain that these structures will not be able to find their equivalent in physical structures in the restricted sense of the word. (SB, 150-151)

As a living (vital) structure, Merleau-Ponty argues that behaviour is irreducible to the physical structures from which the mechanistic interpretation was developed, e.g. the formation of a soap bubble vs the development of an organism. A physical structure is an "ensemble of forces in a state of equilibrium or of constant change such that no law is formulable for each part taken separately [given their fixed causal connections] and such that each vector is determined in

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[140] Given that the organism-environment relation is basic, when we speak of qualities of the organism independently of the environment, or vice versa, we are already doing realistic analysis.

[141] By "organic mereology" of the lived-body, I am specifically referring to Merleau-Ponty's point that the organism is part of the world just as the heart is part of the organism (PhP, 209).

size and direction by all the others." (SB, 137)[142] This is distinguished from vital structures where "the properties of a system are modified by every change brought about in a single one of its parts and, on the contrary, are conserved when they all change while maintaining the same relationship among themselves." (SB, 47) Between physical and vital structures, reductionism and machine-mereology are only appropriate for the former and insufficient for the latter, because we encounter a different kind of systematicity and coordination between organic parts in relation to the organic whole. Against the possibility of reducing vital structures to the structures already present in the physical environment, for vital structures,

> equilibrium is obtained, not with respect to real and present conditions, but with respect to conditions which…*the system itself brings into existence*; when the structure, instead of procuring a release from the forces with which it is penetrated through the pressure of external ones, executes a work beyond its proper limits and constitutes a proper milieu for itself. (SB, 145-146, emphasis mine)

From the structural interpretation of behaviour, it is insufficient for behaviour—especially when we consider its adaptive value—to be restricted as the product of following pre-established nerve pathways. Similar to what Merleau-Ponty argues, I think it is insufficient to understand the adaptive appearance of organisms in terms of pre-existing genes and pathways of gene-expression. For Merleau-Ponty, the adaptive behaviour (and for me, adaptive appearance of organisms) is not merely a "compensatory process" by which organisms passively respond to environmental factors; behaviour can be adaptive because organisms actively maintain themselves in ways that are not already given by its usual manner of engaging with the environment. While similar arguments were already presented under eco-evo-devo (Chapter 2), what I want to show

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[142] In the mechanistic account of behaviour, we see the appropriation of organisms to physical structures when "behavior, it is said, has its roots and its ultimate effects in the geographical environment even though, as has been seen, it is related to it only by the intermediary of the environment proper to each species and to each individual. "How can a cause in one universe of discourse produce an effect in another? All our causal laws refer to events within the same universe of discourse and, therefore, since the geographical environment belongs to the universe of physics, we require its effects [viz. organisms] to belong to it also."(SB, 133)—Merleau-Ponty is quoting (Koffka, *Principles of Gestalt Psychology*, 49).

here is that they are also available to Merleau-Ponty's framework. As Merleau-Ponty notes, organisms *improvise* when they encounter changes and difficulties.

> It has long been known that the dung beetle, after the amputation of one or several phalanges, is capable of continuing its walk immediately. But the movements of the stump which remains and those of the whole body are not a simple *perseveration* of those of normal walking; they represent a *new* mode of locomotion, a solution of the unexpected problem posed by the amputation. …Thus, the reorganization of the functioning is not released automatically by the removal of one or several phalanges as would happen if a *pre-established* emergency device were involved; it is accomplished only through the [presence] of external conditions, and we are led to believe that it is *improvised*. (SB, 39-40, emphasis mine)

In this example, a strictly mechanistic account that depends on the re-assembly of pre-established elements of behaviour would be insufficient to explain how the beetle regains its locomotive capacity, without, at the same time, regenerating its previous morphology.[143] What this example shows us is that we cannot understand behaviour in terms of the fixed morphology of an organism. If we examine our scientific methods that provide evidence for the mechanistic breakdown of an organism, that is, in our attempt to reduce behaviour in terms of pre-established reflexes mapped on a fixed morphology of the organism—what we have actually examined is the organism only in a laboratory setting, or what Merleau-Ponty calls the laboratory organism and laboratory phenomena (and coincidentally, the sick organism). According to Merleau-Ponty,

> The reflex as it is defined in the classical conception does not represent the normal activity of the animal, but the reaction obtained from an organism when it is subjected to working as it were by means of detached parts, to responding not to complex situations but to isolated stimuli. Which is to say that it corresponds to the behavior of a sick organism—the primary effect of lesions being to break up the functional continuity of nerve tissues—and to "laboratory behavior" where the animal is placed in an anthropomorphic situation since, instead of having to deal with those natural unities which events or baits are, it is restricted to certain

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[143] Also see the example of Cnidarians I gave in Chapter 3 (Abrams *et al.*, 2011). Similar to the amputated beetle, amputated *Aurelia* jellyfish do not preserve the same morphology as a "normal" individual, rather than regenerating their bodies (which they are readily capable), *Aurelia* jellyfish address the problem of asymmetry by reconfiguring their bodies to a new body-plan.

> discriminations; it must react to certain physical and chemical agents which have a separate existence only in human science. (SB, 43-44)

While Merleau-Ponty argues that our scientific idea of "elemental reflexes" is improper to the natural conditions of behaviour (i.e. it is a phenomenon induced by experimentation), reflex behaviour nevertheless exist as a special case of organism comportment. The mechanistic account is therefore *insufficient* rather than mistaken when it tries to reconstruct the whole of organism behaviour in terms of what we learn from an experimental setting. Merleau-Ponty writes,

> Thus the reflex—effect of a pathological disassociation characteristic not of the fundamental activity of the living being but of the experimental apparatus which we use for studying it…cannot be considered as a constituent element of animal behavior except by an anthropomorphic illusion. But neither is the reflex an abstraction…the reflex exists; it represents a very special case of behavior, observable under certain determined conditions. (SB, 45-46)

Extending these criticisms to the gene-centric account of organism appearances in general, in its attempt to understand organisms in terms of elemental genes and gene-expression, by isolating and inducing mutations, what we actually study is only the organism under very limited and controlled conditions of experimentation. Rather than upholding a constancy of molecular elements, what we should preserve instead is the constancy of lived-*meaning*, the meaning of a situation for the organism (SB, 44-45).[144] Although mechanism purports to study the organism "in-itself"—in terms of their objectively causal and molecular determinations—from the limitations of realistic analysis which excludes meaningful involvement, mechanistic biology cannot in fact meet its own aims. While it is true that mechanism is founded on the phenomenon

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[144] Merleau-Ponty writes, "What is observed, especially if the animal is placed in a natural situation, is another sort of consistency and another sort of variations. If I catch my toe on a root while walking, the flexor muscles of the foot are suddenly relaxed and the organism reacts by accentuating this relaxation, which will liberate my foot. If, on the other hand, I miss my step while coming down a mountain and my heel strikes the ground sharply before the sole of the foot, the flexor muscles are once again relaxed suddenly, but the organism reacts instantly by a contraction. …Here the variation of the response in the presence of analogous stimuli is related to the *meaning* of the situations in which they appear and, inversely, it can happen that situations which appear different if they are analyzed in terms of physical and chemical stimuli provoke analogous reactions." (SB, 44-45)

of organisms, the mechanistic account only upholds because it takes place at the occasional break down of meaning. This why I think mechanism is insufficient.

4.2 Phenomenological critique of Uexküll's biology

If indeed organisms are meaningfully involved with their umwelten, Uexküll was aware of this when he took meaning as his point of departure for umwelt research. The very aim of Uexküll's biological project and method of participatory observation were to develop a new way of "accessing" organisms that is different from physiology (mechanism), psychology, or appropriation by empathy. While meaningful involvement was covered over under the mechanistic interpretation, Uexküll recognizes that "meaning is the pole star by which biology must orient itself" (FWM, 160). Uexküll's response to the limitations of mechanism is that organisms are subjects who constitute functional/meaning cycles, with feedback relations between their world of action (Wirkwelt) and world of perception (Merkwelt)—the movement of which opens up an interior that is their subject-world, or umwelt.

Unlike either side of the mechanism-vitalism debate, Uexküll's emphasis on meaning in biology precludes him from much of Merleau-Ponty's criticisms as I have discussed above. Nevertheless, I think Uexküll is subject to a different line of criticism when he further takes a position for the *perfect* and *complete* relation of organisms with their umwelten. In doing so, Uexküll exceeds what is warranted from his initial awareness that organisms simply have meaning cycles. His hypothesis presupposes the consonant relation (i.e. fitness) between organisms and their conditions of existence, rather than realizing fitness as an ongoing achievement of organic activity. In their perfect and complete umwelten, the engagement of organisms with their environment takes on fixed relations of meaning, this is problematic because (just like the mechanistic interpretation) it cannot account for biological facts such as developmental plasticity, especially given its adaptive significance. I would also like to suggest that insofar as Uexküll's biology remains Kantian in legacy—that is, given that he maintains the distinction between the *in-itself* (objective noumenon) and *for-itself* (subjective phenomenon)—Uexküll cannot properly get past the basic and common distinction that is also supporting the mechanistic interpretation he criticized.

To address these issues in Uexküll's biology, a phenomenological interpretation of organisms reconsiders the facts from which Uexküll argues in favour of meaning, albeit without making the same theoretical commitments, and therefore avoids running into similar problems. The phenomenological interpretation I develop attempts to retrieve the source of Uexküll's convictions as to why motility and neurosensory systems are the conditions of umwelt formation. My interpretation will also explore Uexküll's convictions at a level that can accommodate plant life and developmental plasticity. Here I think a phenomenological interpretation of organisms can undo the distinction between matter and meaning, and as such, provide us with further insight on how meaning cycles (articulated by Uexküll) can belong to organisms still understood as material entities (articulated by mechanistic biology). Borrowing from Merleau-Ponty, I will argue that it is because organisms are *lived-bodies* that they are open to both the mechanistic and Uexküll's interpretations.

What I mean by "retrieving the source of Uexküll's convictions" is to reconsider the question of how organisms *imply* their umwelten. In other words, from the phenomenon of organisms, from the ways in which organisms show themselves, how do we arrive at the implication that they have umwelten, or that they form meaning cycles? In his lectures on Uexküll, Merleau-Ponty gives a possible response in place of Uexküll that it is organism comportment (as behaviour) which makes the implication of them having umwelten (NL, 175). The behaviour of animals show us that they have subjective worlds distinguished from the objective, mind-independent world of mechanistic biology. Behaviour indicated that organisms are not abandoned to their conditions of existence, because behaviour is a "reply to the external world" (NL, 170). As I already discussed in Chapter 3, I think Uexküll's identification of animal behaviour—which must include locomotion and neuro-sensation—as the condition for having umwelten is problematic because it excludes plant life (as capable of having umwelten) and plasticity (as another instance of umwelt formation). Like behaviour, plasticity allows organisms to mediate their conditions of existence without being abandoned to it. Here I think Merleau-Ponty's account of behaviour, as *comportment*, contributes to the discussion by expanding the criteria of umwelt formation to include problematic cases for Uexküll. What I mean by Merleau-Ponty's idea of comportment is the manner in which organisms conduct and carry themselves in relation to their environment—everything from their development (the plasticity of development) to their ethological behaviour count as features of their comportment. Instead of animal behaviour specified as such, in my view, it is comportment that gives us evidence for organisms in general having umwelten. This does not refute or reject Uexküll's contribution that behaviour *also* shows us the umwelten of animals. To identify comportment as the condition of having umwelten is to open up the scope of what we can admit as meaningful involvement. Specifically for my interests, comportment opens up to the possibility that plants, too, have umwelten and meaningfully engage with their surroundings via developmental plasticity.

Similar to my criticisms of mechanistic biology, here I criticize Uexküll to the extent that I take the scope of his theory to be limited, rather than mistaken. The point at which I think Uexküll *is* mistaken, is when he further makes the hypothesis that organism-umwelt relations are perfect and complete. Still following a phenomenological way of thinking about this problem, there must also be something about the organism-umwelt relation, about organism comportment, that allows for Uexküll's interpretation. For comportment to show us that organisms have perfect and complete umwelten is for it to exhibit what Uexküll describes as the point and counterpoint structure. Recall for example, Uexküll saying "Were the flower not bee-like, and were the bee not flower-like, the consonance could never work" (FWM, 190). Between the comportment of the bee and comportment of the flower (both of which contribute to each other's umwelten), the manner in which they exist—their morphology, colour, perception, behaviour, etc.—is as if they form a musical composition like the voices of a duet; where the whole of nature can be understood as a grand symphony that plays itself. My objection to Uexküll here is that neither the physical environment nor organisms remain constant and unchanging, contrary to his shift between the constancy of objects to the constancy of organism-subjects. If there is such an appearance of fitness, and indeed I think there is, it has to be maintained and achieved by organisms in response to both their own changes (development), as well as the changes that happen in the physical environment. The way in which organisms maintain themselves, and how they achieve their meaningful relations to the environment, is by their lived-bodies.

What I think is correct in Uexküll's umwelt theory is that organisms have both a world of perception and world of action, and together they relate organisms to their surroundings through a cycle of meaning. The meaning cycle as such is always dynamic and feeds back onto itself. What I think Uexküll misses in his formulation is the connection between perception-action and its connection to an entity that *enacts* (or is at least capable of enacting) this relation. Uexküll's theory is limited in that he never attributes the meaning-cycle to a dynamic entity that is capable of maintaining it, rather than simply having it. In my view, what is missing in Uexküll's articulation is the fact that organisms are meaningfully involved as lived-bodies. When Uexküll describes the organism body as a "living house" or "dwelling shell" (FWM, 147), this cannot account for the essential connection between embodiment and perception-action. Further on this point, the connection to embodiment is important because behaviour—as the product made possible by perception-action—"must be anchored to a body" (NL, 140). Despite Uexküll's attention to meaning in biology, without rethinking the body of organisms from the mechanistic framework in which it is usually assumed, I take Uexküll's umwelt theory to lack an essential component for what he aims to argue. It is then to Merleau-Ponty's account of the lived-body that I now turn.

4.2.1 The lived-body and its motricity

To clarify the connection between Uexküll and Merleau-Ponty, the comparison that I would like to draw is that both are after an idea of meaningful involvement. The proper "environment" of organisms is not the physical environment of science, but something meaningfully taken up by organisms, and to which organisms address themselves.[145] When Merleau-Ponty says that organisms have a dialectical relations of meaning to the environment, this is to say that only with reference to a lived-situation—a context of comportment (e.g. Uexküll's idea of *umwelt*)—can we make sense of the organism, their behaviour, morphology, etc. To go beyond Uexküll at this point, in this section I will argue that Merleau-Ponty's theory of the body can better account for the organism-umwelt relation in both its scope and dynamism. From the example of the *Aurelia* jellyfish I discussed in Chapter 3, we saw that bodily asymmetry affects both their usual world of perception (to perceive all around) and world of action (movement by propulsion). Radial symmetry of the body was essential for *Aurelia* to maintain their meaning cycle, both their world of perception and world of action (the two forceps constituting Uexküll's meaning cycle) fundamentally depend on their body structure. The point I now return to make with this example is to emphasize the relation between perception-action and embodiment. I will argue that from Merleau-Ponty's theory of the lived-body, we can develop a more primordial[146] sense of the criteria for having umwelten than Uexküll's formulations, in a way that can accommodate plant life and plasticity.

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[145] This movement of addressing and taking up is the phenomenological idea of *intentionality*.

[146] What I mean by "primordial" here is that from an account of umwelt formation in terms of the lived-body, we can include Uexküll's identification of animal behaviour (locomotion and neuro-sensation) as an umwelt-forming condition.

It was not enough to say that comportment merely implies the umwelten of organisms, comportment also poses an inherent question about the relation between an organism's umwelt and the fact of their embodiment. This is because it is *as* their bodies that organisms comport themselves, what it means to have an umwelt is then to have a particular manner of being meaningfully involved *as a body*. Merleau-Ponty writes,

> One's own body is in the world just as the heart is in the organism, it continuously breathes life into the visible spectacle, animates it and nourishes it from within, and forms a system with it. (PhP, 209)

Organisms form organic systems with the world as the bodies they live. By the lived-body, what I mean is the body that organisms unify and inhabit in the first person (the first organism), by contrast to the physical body of mechanism that is *partes extra partes*. In *Phenomenology of Perception*, Merleau-Ponty offers us an account of the lived-body by examining the experience of space or spatiality. For Merleau-Ponty, we do not come to know space with reference to *positional space*, space is neither an absolute point upon the world, nor is it the relative distance between objects both accounts of absolute and relative space lead the view that the experience of space (the space "for me") is an internal representation of objective spatiality ("in itself"). Instead, Merleau-Ponty argues that we have an original sense of space through our *situational spatiality*, a lived-space that makes an essential reference to my body. The problem with positional space is that it forgoes the condition of possibility for spatial meaning in the first place: it is from my body as the origin of space that I have any sense of spatiality or orientation in space.[147] Merleau-Ponty concludes that what we need is an existential space that is furnished by my lived-body, because my body provides the structure and set-up that is presupposed by any account of positional space. For example,

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[147] Merleau-Ponty writes, "It is easy to show that a direction can only exist for a subject who traces it out, and although a constituting mind eminently has the power to trace out all directions in space, in the present moment this mind has no direction and, consequently, it has no space, for it is lacking an actual starting point or an absolute here that could gradually give a direction [*sens*] to all the determinations of space." (PhP, 258)

> If I am standing and if I hold my pipe in a closed hand, the position of my hand is not determined discursively by the angle that it makes with my forearm, my forearm with my arm, my arm with my torso and, finally, my torso with the ground [i.e. with reference to my body situated in objective space]. I have an absolute knowledge of where my pipe is, and *from this* I know where my hand is and where my body is. …When the word "here" is applied to my body, it does not designate a determinate position in relation to other positions or in relation to external coordinates. It designates the installation of the first coordinates, the anchoring of the active body in an object, and the situation of the body confronted with its tasks. (PhP, 102-103)

From Merleau-Ponty's existential analysis of lived-space, we arrive at both the essential connection between spatiality and the body, and more relevant for my discussion, an acknowledgement of the body as something that can be polarized and oriented towards the world. Following the passage above Merleau-Ponty writes,

> If my body can ultimately be a "form," [i.e. if my body can take on a dialectical gestalt structure] and if there can be, in front of it, privileged figures against indifferent backgrounds, this is insofar as my body is polarized by its tasks, insofar as it exists *toward them*, insofar as it coils up upon itself in order to reach its goal. (PhP, 103)

Entities in the world can solicit and orient my body towards them, and in this way, orientation describes an important manner in which we are involved in the world.[148] If we examine this further, the possibility to be oriented depends on the possibility to "face" (and more elaborately, to move) towards what orients us. What the possibility of orientation reveals is that we live and carry our bodies given what Merleau-Ponty calls our *kinesthetic situation*. As lived-bodies, our original intentionality[149] in the world is not the "I think" of consciousness (contrary to Husserl's phenomenology), but the "I can" of *motricity*—our kinesthetic possibility and original sense of motility and movement (PhP, 139), our character of being towards the world, such that we can

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[148] Merleau-Ponty plays on the different meanings of the term *sens*: as direction (orientation), sense, and meaning.

[149] Here I mean "intentionality" in its phenomenological use. I do not mean intentionality as an act of willing, but our manner of being directed and receptive towards the world.

take up meaningful relations through our comportment. It is to this idea of motricity that I attribute both (ethological) behaviour and developmental plasticity, both are ways in which organisms "mobilize" themselves to modify their relation to the environment, without necessary changing their positional space or the physical environment. In addition, from Merleau-Ponty's idea of motricity I would like to suggest that plants also have kinesthetic possibilities. Just like animals, plants can also orient themselves to their surroundings, e.g. towards sunlight both by their daily movement (circumnutation) and plasticity of body structure (e.g. leaf arrangement).

Given the role of motricity for meaningful involvement, I think we can explain why Uexküll identified motility and behaviour as the conditions of umwelt formation. In my reading of Uexküll, whether or not organisms have umwelten depend on their ability to *perceive* their physical environment, and this is why Uexküll denied the umwelten of plants. To have an umwelt, i.e. to be meaningfully involved in the world, depends on the capacity of an organism to have dynamic *perspectives* of the world, such that organisms can be "toward" some aspect of the environment and "away" from others. While I agree with Uexküll that motility contributes to the dynamic perspectives that organisms can have, I would like to suggest that both motility and behaviour are instances of a more original motor and kinesthetic possibility, which is the organism's motricity. In my view, it is motricity of the lived-body that allows organisms to have dynamic perspectives. What is problematic in Uexküll's account is that the level at which he identified the condition of umwelt formation, namely, restricting umwelt formation to animal behaviour was already too specific, hence the limitations in his theory.

4.2.2 The lived-body as the connection between plasticity and perception

To further lay out the significance of plasticity, I suggest that plasticity not only changes an organism's umwelt by changing the connection between their body and their perspective, it also contributes in *maintaining* organism bodies and their umwelten. Still using Merleau-Ponty's idea of the lived-body, I argue that the work of maintenance by plasticity depends on the essential connection between perception and embodiment, and to relate plasticity with perception strengthens the argument for its significance in umwelt formation. So far I have only discussed the motor and kinesthetic aspects of plasticity without explaining how it relates to perception, it is this relation that I would now like to address.

Indeed, the discussion of motricity already implies an essential connection with Merleau-Ponty's theory of perception. When I perceive something, my view of the object is such that my perspective and my body together orient towards the object *in a single gesture* (PhP, 153). Merleau-Ponty says,

> So that there be something, it must be presented to an incarnated subject, Subjektleib. …When I perceive an object, I am aware of the motor possibilities [kinesthetic situations] that are implied in the perception of this thing. The thing appears to me as a function of the movements [motricity] of my body. (NL, 74)

We "live" our bodies because we have an inherent awareness of our perceptual and motor unity, this Merleau-Ponty calls our *body schema*. I have an awareness of my body not through neuro-sensation, but via my body schema which coheres my senses (perception) and my motor possibilities (motricity) together with the flesh that is my body. For example, I can perceive and know the whereabouts of an itch not by laying out my body as an object, and locating the itch before me in positional space, rather, I know it (and in a sense "see" it) by the unity of my body schema. For Merleau-Ponty, perception coincides with our embodied perspective of the world in a kinesthetic situation, that is, our perception entails the motricity of our body. If I want to see the "back" side of a cube, this requires a different kinesthetic situation of my body than perceiving its "front" side,

> if I bring the object closer to me, or if I turn it around in my fingers in order to "see it better," this is because every attitude of my body is immediately for me a *power for a certain spectacle*, because each spectacle is for me what it is within a certain *kinesthetic situation*, and because, in other words, my body is permanently stationed in front of things in order

> to perceive them and, inversely, appearances are always enveloped for me within a certain bodily attitude. (PhP, 316, emphasis mine)

Perception is always perspectival, and this perspectival structure is grounded in the fact of our embodiment. From this I would like to suggest that developmental plasticity contributes to umwelt formation because of the connection between the body and perception. Since perception and the body are oriented "in a single gesture", and given that the umwelt of an organism is a cycle of meaning between their world of perception/action to the environment, plasticity of the body implies change to an organism's perspective upon the world, and in turn, their relation of meaning to the environment. Merleau-Ponty writes,

> every perception of a thing, of a form, or of a size as real, or that every perceptual constancy sends us back to the positing of a world and a system of experiences in which my body and the phenomenon would be rigorously connected. (PhP, 317)

It is *as* lived-bodies that organisms are meaningfully involved in the world. Plasticity of the body, as dynamism of the body, is a way in which organisms further *maintain* a consistent way of meaningful involvement. Merleau-Ponty gives the example of being at an art gallery to show the bodily role of maintaining a perspective; when we look at paintings, they have for us

> an optimal distance from which it asks to be seen—an orientation through which it presents more of itself—beneath or beyond which we merely have a confused perception due to excess or lack. …The distance between me and the object is not a size that increases or decreases, but rather a tension that oscillates around a norm. …There is a point of maturity of my perception that at once satisfies these norms and toward which the entire perceptual process tends. (PhP, 316)

Similar to the contributions that our bodies bring to maintain optimal or privileged perspectives of an object, I think organism umwelten—that is, certain privileged and preferred ways of meaningful involvement for an organism—are also the achievement of their bodily comportment. Specifically by developmental plasticity, as we saw in examples of invasive plants, organisms can maintain an optimal experience (e.g. of environmental resources) without changing the physical environment itself. The meaningful cycles that organisms have with the environment is not something static, as they would be if they are perfect and complete, but as Merleau-Ponty tells us, "oscillate around a norm". Just as we *acquire* the fixity of objects through dynamic perception, the "perfect and complete" relation between organisms and their umwelt is also an acquired one. The work of maintaining umwelten, specifically through plasticity, depends on the connection between perception and embodiment. Through this connection, plasticity is an exercise of an organism's motor possibilities (motricity), it allows organisms the dynamism required for having *perspectives* of their surroundings, both drawing a distinction from an absolute perception of the environment (which would be a view from everywhere and nowhere), and maintaining the situation in which "objects" can appear. In relation to the impediments that organisms can encounter in their experience of their surroundings, plasticity is then part of an organism's adaptive repertoire, especially for plants, to relate to their surroundings in a favourable or privileged manner.

By Merleau-Ponty's account of perceptual constancy, here I think we can also provide an alternative interpretation for why Uexküll believed in the perfect and complete relation between organisms to their umwelten. While Uexküll favours the constancy of subjects over objects (FWM, 198), the real problem is not a manner of locating constancy in either objects or subjects, assigning it either to the physical environment or the meaning-giving subject. Instead, our concerns is how constancy and consistency come to be, and how anything *can* present itself as constant in the first place. To this Merleau-Ponty argues that our embodied perception is the source of their constancy, the constancy of what appears (be it its form, size, colour, etc.) is a product of our dynamic involvement in the world, it originates from the norm of our perception that furnishes us with the experience of constancy in the first place. Constancy and fixity are then acquired features, it should not be presupposed either on part of objects as a reality "in-itself" (e.g. the mechanistic conception of the physical environment), or the world-constituting subject by which everything is "for-us".

4.3. Joint critique of mechanism and Uexküll

Having introduced Merleau-Ponty's idea of the body, its motricity, and the perspectival character of having umwelten, this leads to what I consider to be the common problem with both mechanism and Uexküll: (1) both consider the organism body by what Merleau-Ponty calls a *congealed anatomy*, and (2) both uphold an *in-itself, for-itself* distinction.

4.3.1 Dynamism of the lived-body and the problem of "congealed anatomy"

On the one hand, mechanism and Uexküll have inadequate interpretations of organisms because organism comportment, especially developmental plasticity, requires a dynamic anatomy of the organism body. The example that Merleau-Ponty gives is the ameba (NL, 170), depending on whether they are feeding or moving, amebae can actively change their morphology to fit their behaviour. An ameba is never both feeder (with vacuoles acting as their stomach) and mover (with pseudopods acting as legs) at the same time, each depends on the "flowing protoplasm" of the ameba that endlessly re-creates its body plan in relation to the behaviour it enacts.[150] In their self-maintenance, organisms take on the *appearance* of machines with pre-established bodies (mechanism) and pre-established relations of meaning (Uexküll), however, each organism

> is in effect surrounded by a *protoplasm capable of plasticity*. The unity of the organism does not rest on the central nervous system; it must rest on an activity. (NL, 170, emphasis mine)

What this example of the ameba motivates is a new understanding of organic morphology. From Merleau-Ponty, morphology is not the static form of an organism *solidified* as a strictly physical entity; in its living significance, morphology is rather the body *stabilized* in its dynamism for a particular mode of comportment (NL, 168). We cannot sufficiently understand comportment if it

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[150] [optional] Merleau-Ponty writes, "Amoebae: these are in appearance animals made of "flowing protoplasm." They do not have defined organs; at every instant, the amoeba is made of pseudopods (legs) or vacuoles (stomach), and then makes them disappear in order to recreate them. …The *Bauplan* is endlessly recreated. …For the amoeba, to maintain itself and to function are the same thing." (NL, 170)

is anchored to organisms with congealed anatomy, only by their dynamism (albeit as postures for many organisms) is comportment possible.

Improving upon Uexküll's attention to meaning in biology, it is with this idea of the dynamic lived-body that I think Merleau-Ponty's account can accommodate the role of plasticity in umwelt formation. While Merleau-Ponty was likely not aware of developmental plasticity, the point of significance I find in his discussion of the lived-body is its connection to the meaningful involvement (i.e. for umwelt formation) of organisms with their environment. By means of plasticity—which I interpret as an instance of the motricity of comportment—organisms can change or stabilize the manner in which they are meaningfully involved with the environment as their bodies.

4.3.2 Problem of the in/for-itself distinction

On the other hand, organism comportment and perception show us that they are neither purely "innate" (immanent) phenomena manifesting from the organism for-itself—organisms can be solicited and react to the world—nor are they impositions from an "objective" (transcendent) environment in-itself. Merleau-Ponty writes,

> We cannot remain within this dilemma of understanding either nothing of the subject or nothing of the object. We must rediscover the origin of the object at the very core of our experience, we must describe the appearance of being, and we must come to understand how, paradoxically, there is *for-us* an *in-itself*. (PhP, 74)

Comportment and perception cannot be secluded to either side of what is exclusively in-itself *or* for-itself, as matter *or* meaning, pure activity *or* passivity. While the mechanistic interpretation maintains these distinctions in its account of the organism as a physical object (and denying any subjective qualities about organisms), Uexküll too maintains this distinction insofar as his biology is a continuation of Kantian philosophy.[151] From Merleau-Ponty's ideas of the lived-body and passivity, I suggest that we can improve upon Uexküll's attention to meaning in biology, without at the same time neglecting the fact that organisms take on a physical existence. What we need in this case—which I think Merleau-Ponty achieves by attributing comportment and perception to the lived-body—is to reconcile the difference between matter and meaning that is presupposed by both mechanism and Uexküll. It is as lived-bodies that organisms take on their corporeality while bearing meaning, and it is to the lived-body that organism comportment and perception properly belong.

Further on the point that organism comportment and perception cannot be explained in terms of pure activity or passivity, I suggest that what we need to articulate is a sense of activity and passivity that do not oppose each other as antitheses, but share a mutual dependence without subordination.[152] Merleau-Ponty tries to clarify this sense of activity-passivity with the phenomenon of sleep, he writes,

> It is necessary to grasp what it is *to sleep*—falling asleep—in a sense an *act*, pressed by a verb—When I lie down I do something, I not only await sleep [in a purely passive manner], I *lend myself to sleep*. (IP, 142)

With sleep as our example, what Merleau-Ponty shows us is that our traditional conception of passivity, activity, and their differentiation are insufficient in the face of organism comportment. Sleep is not an activity, in the sense that we cannot "execute" sleep, or intend ourselves to fall sleep the way we can intend to eat, yet it is nonetheless something that organisms *do*, and as such, sleep is also not passive. In our consideration of organism comportment—i.e. how organisms conduct themselves in relation to their context of existence—it is not enough to simply reverse the

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[151] Again, Uexküll upholds the Kantian noumena-phenomena distinction, which I take as a variation of the object-subject difference.

[152] See Merleau-Ponty's *Institution and Passivity* lectures: "The notion of passivity should lead us to conceive a genus of being that shows the deficiencies of the traditional conceptions of the Subject. Thus the phenomena that have been the main object of investigation seem, if they don't have the function of being examples, at least to provide materials in service of an ontology that is liberated from the opposition of the In-itself and the For-itself." (IP, xxix)

activity-passivity dynamic between organisms and the environment. To say something more subtle than Uexküll's account of the meaning cycle, we should clarify that neither organisms nor the environment are exhaustively constituting or constituted by the other, the manner in which organisms have umwelten is

> not by submitting merely to an external force, but by considering as an external that which comes from ourselves.[153] There is no longer consciousness of what we do, of our significations, on the one hand, and of what the surroundings bring, on the other hand, but rather a confrontation of both… There is an alliance or complicity of our significations with the givens. We are at the mercy of (vague) suppositions, of the swarming impressions, and they are at the mercy of what we attempt to make them [signify]. (IP, 143)

Here I think we can use Merleau-Ponty's account of passivity-activity to improve both the mechanistic and Uexküll's account of the organism-environment relation, for the reason that Merleau-Ponty is attentive to the mutual "alliance" of organism and environment without reducing one as the product of the other. While mechanism is inadequate in that it takes the environment as "actively" imposing selection pressures upon organisms, or for Dawkins, where aspects of the environment are the products of genes and gene-expression, I think Uexküll's account is also inadequate given his Kantian commitments to the organism-subject that constitutes the environment in terms of its world of experience. Contrary to both mechanism and Uexküll, I think it is useful to apply Merleau-Ponty's account of passivity-activity to make sense of the organism-environment relation—a relation by which neither organism nor environment should be submitted as a product of the other.

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[153] I would like to add here: this "external that comes from ourselves" nevertheless retains its externality as something that we do not constitute or create out of ourselves.

Conclusion

In this thesis I have tried to develop a phenomenological interpretation of organisms by showing how we can understand them in terms of Merleau-Ponty's ideas of comportment, the lived-body, and the passivity-activity relation. Returning to my motivations for this project, what I wanted to show is that via a phenomenological interpretation of organisms, we can elaborate on their particular manner of meaningful involvement with the environment. To this end I have argued that organisms are meaningfully involved in the world *as their* bodies, and such an account is valuable because it allows us to criticize mechanistic biology without further committing us to vitalism. By applying Merleau-Ponty's idea of the lived-body to organisms, I tried to show that we find a reconciliation of the object-subject distinction—each side of which is, respectively, the point of focus for mechanistic biology and Uexküll.[154] To condense what I have argued with Merleau-Ponty's conclusion in *The Structure of Behavior*,

> The natural "thing," the organism, the behavior of others and my own behavior [make sense] only by their meaning [contrary to mechanistic biology]; but this meaning which springs forth in them is not yet a Kantian object [contrary to Uexküll]; the intentional life which constitutes them is not yet a representation [but the "towardness" and motricity of comportment]; and the "comprehension" which gives access to them is not yet an intellection [but a more primordial act of perception]. (SB, 224)

Additionally, with a phenomenological interpretation of organisms I have tried to overcome certain limitations posed by developmental plasticity for mechanistic biology and Uexküll. By contrast to the "congealed anatomy" of organisms they both presuppose, I tried to show the dynamic anatomy of the organism body as a lived-body; it is by the *motricity* of the lived-body (the original "I can" in the world) that founds plasticity as well as behaviour in its ethological sense.

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[154] The object-subject distinction took on many forms in the course of my discussion—as the difference between matter and meaning, what is in-itself and for-itself.

To conclude this thesis, I will recapitulate my main points of arguments and draw out more explicitly some implications from my phenomenological account of organisms. I will begin by returning to my discussion of Uexküll's Umwelt Theory. I then elaborate on some implications for the Modern Synthesis and gene-centrism, and eco-evo-devo and Niche Construction Theory. Next, I discuss how my phenomenological interpretation of organisms differs from philosophy of biology, specifically, Walsh's account of *Situated Darwinism*. Lastly, I consider some short comings and unanswered questions for my phenomenological interpretation of organisms.

Uexküll and the *institution* of umwelten

In chronological order of their historical development, first I would like to return to my discussion of Uexküll's Umwelt Theory. Recall that for Uexküll, biology proper should expand in two directions the results of Kantian philosophy, (1) we should examine the role played by our bodies in constituting umwelten, and further, (2) the umwelten of other organisms. Uexküll's central thesis is that organisms relate to their conditions of existence by their subject *function/ meaning cycles* (see Figure 2). In Chapter 4, I used Merleau-Ponty's idea of the passivity-activity relation to criticize Uexküll for his commitment to Kantian ontology. As I tried to show, Uexküll does not give a sufficient account of organisms' meaningful involvement because of his assumption of the object-subject (noumenon-phenomenon) dichotomy. I also took issue with Uexküll's hypothesis of the perfect and complete relation between organisms and their umwelten.[155] While Uexküll contributed to my general development in this thesis (viz. organisms are bearers and investors of meaning), I think his Umwelt Theory is nevertheless limited given his inability to account for plant examples, and how organisms *maintain* themselves and their

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[155] Even though Uexküll was aware that there can be dissonant interactions (the sufferance/tolerance of meaning), he did not consider the implications of dissonance for his Umwelt Theory. What we have to explore then, is how there can be struggle *within* the subjective worlds of organisms.

meaning relations.[156] To address these problems in Uexküll, I used Merleau-Ponty's theory of lived-body to show that organisms in general, including plants, maintain their meaning relations via their bodies and bodily plasticity.

Here I think we can further clarify Uexküll's idea of umwelten and umwelt formation with something that I did not discuss in this thesis; from Merleau-Ponty's idea of institution, I would like to suggest that umwelt formation is a matter of organisms *instituting* their umwelten. Institution is the deposition of meaning that establishes a possibility for repetition; there is a "double aspect of institution, it is itself and beyond itself, restriction and openness." (IP, 12). Merleau-Ponty writes,

> institution [means] establishment in an experience of dimensions (system of references) in relation to which a whole series of other experiences will make sense and will make a *sequel*, a history. The sense is deposited (it is no longer merely in me as consciousness, it is not re-created or constituted at the time of recovery). But not as an object left behind, as a simple remainder or as something that survives, as residue. [It is deposited] as something to continue…without it being the case that this sequel is determined. (IP, 9)

I suggest that organisms institute their umwelten because what it means to form umwelten is for organisms to establish meaning relations (and manners of involvement) with the environment, meaning relations that can *repeat* in the form of biological "signs" or "cues". Organisms institute their umwelten because their meaning cycles are not "merely in [them] as consciousness", if this were the case, there would no *cycle* between organism and environment; moreover, given that we say organisms *receive* cues or triggers from the environment, meaning cycles are also not "re-created at the time of recovery". Without already committing to a narrative whereby organisms "constitute" their umwelten (and in turn, to say that umwelten are "constituted" by organisms), I would like to further examine the sense in which organisms

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[156] Maintenance on part of organisms is required given that the physical environment itself is often changing; in this case, I tried to consider how organisms are able to maintain a consistent *experience* of their environment regardless of physical differences.

institute their umwelten. In his lecture notes, Merleau-Ponty draws a distinction between what is "constituted-constituting" and "instituted-instituting" (IP, 6). We can clarify their difference with my previous discussion of passivity-activity; what *institutes* does not "produce" the *instituted* as an extension or "effect" from itself. Between the instituted-instituting, they take on a passivity-activity relation of mutual contribution rather than composition. It is in this sense that I think Merleau-Ponty's idea of institution can better depict the "echoes, exchanges, symbolic accumulation" (IP, 15) that Uexküll tries to convey in his Umwelt Theory of the organism-environment relation.

Implications for the *Modern Synthesis* and gene-centrism

To distinguish phenomenology from the usual criticisms of mechanistic biology (e.g. from vitalism or scientific alternatives to the Modern Synthesis), I have tried to show that phenomenology allows us to criticize mechanistic biology in a more subtle manner. We have to be careful in that the Modern Synthesis and gene-centrism are nevertheless *justified*, given that they also derive their evidence from the way in which organisms show themselves; indeed, there is a plethora of phenomena to which Modern Synthesis has proven its explanatory suitability.[157] In this case, I tried to show that the benefit of a phenomenological interpretation is that we criticize the Modern Synthesis and gene-centrism for their *limitations*, specifically for their elision of meaning, rather than their correctness *per se*. I also tried to show that many ideas of the Modern Synthesis and gene-centrism claim more than what is warranted from their own mechanistic beginnings (reductionism and machine-mereology). With phenomenology, we are able to account for the implicit and tacit appeal to meaning in the Modern Synthesis, despite its own rejection of meaning, and further explain the reason of its success; this is because the Modern

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[157] Adducing an example I did not discuss in Chapter 1, the gene-centrism account of evolution can best explain *intragenomic conflict* between genes of an individual or individuals (e.g. parents that contribute to the genetic constitution of their offspring).

Synthesis itself developed out of the phenomenon of organisms. In general, phenomenology thus allows us to problematize scientific theories from the same factual sources by which they support themselves.

In developing a phenomenological interpretation of organisms, I extended the following ideas from Merleau-Ponty: (1) the organism body as a *lived-body*, (2) developmental plasticity as founded upon an organism's *motricity*, and more generally, as a feature of organism *comportment* (which takes on a *dialectical gestalt structure*), and (3) a reassessment of the *passivity-activity relation* between organisms and the environment. With them I would now like to show how we can re-interpret various components of the Modern Synthesis and gene-centrism, specifically the following that I discussed in Chapter 1: Weismann's germ-plasm theory, the genotype-phenotype distinction, Mendelian genetics, the neutral theory of molecular evolution, and molecular genetics comprised of DNA sequences.

- *Mendelian genetics.* From a phenomenological point of view, the Mendelian analysis of organisms into discrete, "particulate" traits and genes only articulated a partial truth. If indeed organisms *live* their bodies, what we overlooked from Mendelian genetics is the *organic mereology* of organisms; an interpretation of organisms as lived-bodies implies that they are more than physical assemblages of parts (e.g. Mendelian traits or genes) that accord with the mereology of machines. As lived-bodies, organisms take on both a physical and meaning-bearing existence, and Mendelian genetics applies to organisms only in account of the former. Also to assess it by its own terms, Mendelian genetics is important for the Modern Synthesis because it clarified the mechanisms of inheritance, specifically by showing us evidence to address the problem of blending. From a phenomenological point of view, we can still admit that organisms are open to Mendelian analysis; however, returning to the phenomenon that prompted our theories of inheritance, we should not forget that heredity is originally about the apparent resemblance between parents and offspring. We can further say that resemblance is important because it preserves certain ways in which organisms engage with the environment (as their bodies), the passing on of traits or behaviours is really a passing on of *relations of meaning*, adaptive relations with the environment being an instance.[158]

- *Molecular genetics, the DNA constitution of genes, and the Central Dogma*. For the Modern Synthesis, what the discovery of DNA structure and its mechanisms of replication illuminated is the mechanism of heredity at the molecular level. Again, from a phenomenological interpretation of organisms our effort is to retrieve the phenomenon that gave rise to our theories of heredity, prior to its molecular or Mendelian analysis, and in this case, to clarify the concept of heredity in a way that does not allow its reduction to DNA sequences. Although knowing the structure and sequences of DNA, and knowing the direction in which DNA is replicated (viz. the Central Dogma) definitely contributes to our understanding of genetic inheritance from a molecular level, we should remember that heredity is not only the passing of genetic "information" in the form of DNA sequences. From a phenomenological point of view, heredity is first about the resemblance between parents and offspring, and in turn, how their lived-bodies secure relations of meaning with the environment.

- *Neutral theory of molecular evolution*. Regarding the neutral theory of molecular evolution,[159] we can reinterpret it in terms of the "dialectical gestalt structure" of organism comportment. Recall that what we meant by a "dialectical gestalt structure" is that organisms are addressed to the environment with reciprocations of meaning. We can make sense of organism development, morphology, behaviours, etc. only if we consider them with reference to their

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[158] This is if we if we assume that their conditions of existence remain (at least functionally) the same between parents and offspring.

[159] The central thesis of the neutral theory of molecular evolution is that at the molecular level, molecular changes to DNA sequences tend to be neutral—they are neither adaptive nor maladaptive with regards to the survival and reproduction (fitness) of organisms.

biological context—a background against which organisms show themselves. The neutral theory of molecular evolution also takes on this structure because neutral molecular changes or neutral evolution can only be determined in a contextual manner. Neutrality is possible because genes are to the organism (or to the cell) in a figure-ground relation. If there are molecular changes that constitute neutral evolution, a proper sense of neutrality depends on the conditions of a gene against the background of the organism body, and on a larger scale, the situation of an organism in an ecological context.

- *The phenotype-genotype distinction.* While the Extended Synthesis also criticizes the Modern Synthesis for its account of organism phenotypes (phenotypes are not only the causal product of underlying genotypes), by giving a phenomenological interpretation, I consider organism appearances without already adopting the scientific narrative of phenotype and genotype. For both the Modern Synthesis and Extended Synthesis, “phenotype” is a catch-all term for what we can observe about organisms, what they look like, and how they behave. One reason that I find this distinction problematic is because these descriptions of organisms are as if we are examining mere physical objects. What we forget is that organisms *live* their features with evolutionary import, and that the appearance of an organism is often an “appearance-*for*-comportment”,[160] hence, the features of an organism are not analogous to what we describe of any physical object, but as something that bears meaning. It is further problematic to understand the observable features of organisms as “phenotypes”, because “phenotype” already commits us to the causal connection to genes. Although I would not deny that there is a connection between organism appearance and their genetic constitution, as lived-bodies, this connection should not be interpreted as allowing organisms to be reducible and reconstructable from their genes; what we should also keep in mind is the passivity-activity

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[160] I am referring to Merleau-Ponty’s example of the amoeba that takes on a different morphology depending on whether it is feeding or moving.

relation between genes and the appearance of organisms. Returning to the appearance of organisms prior to its understanding as phenotypes, we should re-examine the manner in which organism appearances relate to genes *before* establishing this relation as a causal one.

Contributions to the *Extended Synthesis*

Through Chapters 2 to 4, I tried to develop three progressive articulations of the meaningful involvement between organisms and their environment. Beginning with eco-evo-devo (EED) and Niche Construction Theory (NCT), organisms are involved with the environment by their *reciprocal causation*.[161] While EED emphasizes the causal impact of the environment on organisms, NCT focuses on the way in which organisms causally impact the environment. Although it is useful that these theories gave us empirical evidence to criticize the Modern Synthesis, I suggest that my phenomenological interpretation still tries to go beyond their scope of critique. For one, I have tried to show that similar criticisms of the Modern Synthesis were also available to Merleau-Ponty's account of organism comportment. What EED, NCT, and Merleau-Ponty all argue for is that we should not presuppose fixed morphologies or behaviours on part of organisms, or pre-existing environmental problems to which organisms later respond. As a matter of fact, organisms often *improvise* (their bodies, their conduct, etc.) to engage with the environment in an adaptive manner organisms are adaptive because they continually *maintain* themselves in the face of environmental changes or changes to themselves, and they do so in ways that are not already determined by a fixed morphology, or predefined possibilities of comportment.[162]

Despite these points of similarity, I would like to suggest that my phenomenological account further contributes to the discussion of organisms by going beyond EED and NCT. As themselves

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[161] For more about the Extended Synthesis see (Laland *et al.*, 2015).

[162] The specific examples I am referring to in Merleau-Ponty are his discussion of the amputated beetle (see SB, 39-40) and the amoeba (see NL, 130).

scientific theories, there are limitations to what EED and NCT are able to criticize in the Modern Synthesis; indeed, they all have in common many basic core assumptions. For example, EED retains the phenotype-genotype distinction (or at least this narrative) in its discussion of developmental plasticity; plasticity is nevertheless studied and referred to in terms of the *norm of reaction* of a gene, a measure of a differential gene expression against various environmental conditions. From a phenomenological point of view, I have instead tried to consider plasticity for the connection it makes between the organism body and their world of perception. While Sultan showed us *that* plasticity contributes to experiential niche construction, my discussion further clarifies *how* this is the case, namely, plasticity contributes to experiential niche construction because the organism body—as a lived-body—bears an essential connection to an organism's world of perception. It is because our bodies and our perspectives are oriented *in a single gesture* that plasticity of the body also modifies our experiences of the world.

Another benefit of a phenomenological interpretation is that we can account for both the Modern Synthesis and NCT understanding of the "environment"—as either a space constituted by physical objects, properties, and forces (a space *in-itself*), or a space of organism niches (a space *for* the organism). From a phenomenological point of view, we can recognize both accounts of the environment without denying them in terms of the other. What phenomenology reintroduces is the sense in which the environment is a niche (as the meaningful lived-situation of an organism), without denying that it also appears as a physical space and "environment at large". Because organisms are lived-bodies, the spatiality of an organism takes on a *double horizon* of physical and bodily space. Merleau-Ponty writes,

> With regard to spatiality, which is our present concern, one's own body is the always implied third term of the figure-background structure [of perception], and each figure appears perspectivally against the *double horizon* of external space and bodily space. (PhP, 103, emphasis mine)

While I agree with NCT that we should consider the "niche" of an organism for its evolution, this is not a backhanded rejection of the physical space to which the Modern Synthesis refers.[163] As is the case for comportment and perception, the "environment" of an organism cannot be understood as either *in-itself* or *for* the organism;[164] a phenomenological interpretation shows us that perception, comportment, and the environment are all "*for-us*, *in-itself*" or "*in-itself, for-us*" (PhP, 74).

How phenomenology differs from philosophy of biology

Above I have tried to distinguish the phenomenological interpretation of organisms from scientific and historical alternatives, here I would like to briefly compare and contrast my interpretation with that from contemporary philosophy of biology. I will discuss Walsh's theory of *Situated Darwinism* as my example.[165] I pick Walsh in particular because—compared to modern trends in philosophy of biology, e.g. naturalism, or arguing for the existence of emergent phenomena—Walsh presents a very different kind of argument for the role and proper place of organisms in evolution. Walsh defends organisms against mechanistic biology in terms of their agency, purposiveness, and a "naturalized teleology", for Walsh, "evolution is adaptive because *organisms* are adaptive, goal-directed systems"[166] that interact with their environment via their *affordances*. In this section I compare Walsh's account of organism affordances to the phenomenological idea of meaning, organism *purposiveness* to the discussion of intentionality as

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[163] If we want to criticize the Modern Synthesis account of the environment, for phenomenology, we must show how—from our lived-space that is more primordial than physical space—the Modern Synthesis arrives at its interpretation.

[164] Organism comportment is neither an internal, unsolicited drive of the organism (for-itself), nor is comportment the product of environmental forces (in-itself). Similarly, perception is neither an internal projection of organisms, nor is it imposed by an external environment.

[165] From Walsh, *Organisms, Agency, and Evolution* (2015).

[166] (Walsh, 203, emphasis mine).

motricity, and implications of my discussion on the passivity-activity for Walsh's account that organisms are *agents* of evolution.

The term affordances was coined by psychologist J. J. Gibson to describe the manner in which the environment is perceived by a subject; affordances come about via the organism-environment relation, whereby features of the environment are perceived in their possibility *for* the organism.[167] For example, if we speak of a supporting surface, we can describe it physically in terms of it being horizontal, flat, or rigid; however,

> an affordance of support for a species of animal have to be measured relative to the animal. They are unique for that animal. They are not just abstract physical properties. They have unity relative to the posture and behavior of the animal being considered. So an affordance cannot be measured as we measure in physics. Terrestrial surfaces are also climb-on-*able* or fall-off-*able* or get-underneath-*able* or bump-into-*able* relative to the animal." (Gibson, 120, emphasis mine)

Affordances are features of the environment that organisms perceive in their own ability for action; for Walsh, it is in this sense that having affordances already entail that organisms are *purposive agents*. This is not to say that organisms are *cognitive* agents; rather, Walsh argues that we must recognize them as purposive systems and "agents of a sort". He writes,

> an affordance is a joint property of a purposive system [the organism] and the conditions with which it interacts [the environment]. Affordances are opportunities for, or impediments to, the pursuit of a system's goals. Affordances thus imply agency. Only agents experience their conditions as affordances, and conversely, conditions can only afford opportunities or impediments to agents. In this way, the alternative I shall outline introduces the organism as agent into evolutionary thinking. (Walsh, 163)

Given that organisms have affordances and relate to their conditions of existence via affordances, what this means is that organisms engage with the environment through a function

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[167] See Gibson's *The Ecological Approach to Visual Perception* (1979). He writes, "The affordances of the environment are what it offers the animal, what it provides or furnishes, either for good or ill. …I mean by it something that refers to both the environment and the animal in a way that no exist ing term does. It implies the complementarity of the animal and the environment." (Gibson, *The Ecological Approach to Visual Perception,* 119)

of their own "ability-for", and this is why organisms are purposive systems and agents.[168] In more detail, Walsh argues that organisms are purposive agents because they meet the following two conditions, (1) organisms *experience* their condition of existence in terms of affordances, such that organisms are "capable of responding to propitious conditions as propitious by exploiting them, and to unpropitious as unpropitious, by ameliorating them." And concomitantly, (2) organisms also have an *adaptive repertoire* such that "on any occasion, there must be a range of possible outcomes or activities that the system or its parts could implement" (Walsh 163-164).

In my own discussion of organisms, I also focused on the fact that organisms have experiences and adaptive repertoires (via developmental plasticity). However, by contrast to Walsh's appeal to affordances, purposiveness, and organisms as agents, my phenomenological consideration lead to an account of organisms as meaningfully involved with the environment as lived-bodies. Rather than affordances, I argued that organisms engage with the environment by relations of *meaning*. At first glance, affordances and meaning are similar in that both posit a basic—albeit very diluted—sense of purposiveness or towardness, or as phenomenologists say, intentionality. Walsh describes the environment perceived by organisms in terms of its "ability-for" the organism (e.g. climb-on-ability of a rock), I read this to be similar to Merleau-Ponty's idea of our bodily-intentionality, i.e. our motricity and our attitude of "I can" towards the environment;[169] both Walsh and Merleau-Ponty also argue that the naturalized purposiveness of organisms is not cognitive in its origin.[170] Here I suggest the key point of difference is that Merleau-Ponty further specifies *how* organisms are purposive (i.e. the manner in which they have relations of meaning, intentionality, orientation, or towardness), namely, because organisms are lived-bodies. Meaning is fundamentally connected to embodiment; it is because we live our

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[168] I use "ability-for" to capture both the agentive and purposive quality that Walsh attributes to organisms.

[169] These are also similar to Uexküll's idea of *functional tones*.

[170] The purposiveness and intentionality of organisms is not something "for" the organism as a consciousness or cognitive agent.

bodies that we have the meaning relations we do. Although Walsh discusses the organism body (and bodily differences between organisms) in many of his examples, he does not explicitly make the connection between affordances, purposiveness, and embodiment.[171]

The idea of meaning also differs from affordances in that meaning—specifically as meaningful comportment—takes on a *structure*; meaning relations between organism and environment show up in a dialectical, gestalt, figure-and-ground manner. Even if we accept *that* organisms have affordances, reading Walsh, it is uncertain *how* this is the case, or *in what manner* organisms afford the environment. This is indeed a central question for Walsh, as he notes in concluding his book, "the questions of most pressing importance for evolution revolve around the ways in which organisms constitute and hold in place the conditions for evolution" (Walsh, 247), which is to say, how organisms hold in place their affordances with the environment. To this I would like to suggest that organisms maintain their affordances as their bodies, taking on a dialectical gestalt structure with the environment, and not forgetting the passivity-activity relation therein.

Phenomenology therefore tries to go beyond standard considerations in philosophy of biology for the reason that it attends to the manner in which something shows up—how organisms phenomenalize, and in turn, how they provide evidence for our theories. If it is organism comportment that shows us they have affordances,[172] I think a closer examination of organism comportment goes against Walsh's idea that organisms are *agents* of evolution. For Walsh, organisms are agents because they are "purposive, self-synthesising, self-regulating entities, open systems, constantly exchanging matter and energy with their

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[171] For example, Walsh discusses the bodily differences between a paramecium and porpoise (a close relative of dolphins), and he notes that their different bodies in turn figure into their different *experiences* of water viscosity. However, in these discussions Walsh does not explicitly draw the link between the organism body and their perceptual/experiential environment (Walsh, 171).

[172] I suggest that it is organism comportment that shows us their affordances because it was also comportment that showed us their relations of meaning.

environments" (Walsh, 163). It is on this point of agency that Walsh contrasts his account of organisms with the mechanistic interpretation (organisms as objects) presented in the Modern Synthesis and gene-centrism. Here I think it is not enough for Walsh to say that organisms are *self*-making or *self*-maintaining. While this may appear to be the case given their capacity for niche construction and developmental plasticity, what we forget is that organism activities in fact presuppose a *context* in which they take place. Just as genes do not express themselves without the conditions of the cell and organism, so too, organisms do not contribute to their persistence without an environment to which they are addressed.

What I think we should more carefully consider in Walsh's account is the organism-environment relation without subsuming the environment as a product of organism-agents. To bring back my discussion of passivity-activity, another point of difference between meaning and affordances is that meaning is both *in-itself* and *for-the-organism*. Unlike affordances that are taken up only in them being "for" organisms, meaning is neutral with regards to the in-itself and for-itself distinction because it is both. Meaningful relations between organism and environment are neither strictly imminent (to the organism) nor transcendent (as an external, objective environment). If our task is to reinstate the role of organisms in evolution from their gene-centric dismissal, we must also prevent ourselves from going too far in the opposite direction, that is, as if organisms are agents that constitute the environment by their own affordances.

Limitations and future considerations

To conclude by re-emphasizing my motivation for a phenomenological interpretation of organisms, what I have tried to explore is the capacity of phenomenological concepts to illuminate our understanding of organisms beyond our usual accounts in scientific biology and philosophy of biology. Here I would like to reflect on the limitations of my project and make some suggestions for further consideration.

A central point of focus in my thesis is the *phenomenon* of organisms; organisms give evidence to our theoretical understandings *from* the ways in which they show themselves. This is why Merleau-Ponty argued in favour of phenomenal priority, and this is why I characterized my effort as an act of return or retrieval. To clarify, I do not mean to say that everything we can know is already contained in the phenomenon of organisms (as if we know them by Platonic recollection), rather, I mean that the *evidence* supporting our interpretations—interpretations which are various and at times contradicting each other—trace back to a phenomenal source. What I think is uncertain in my account is how we should further research organisms from a phenomenological point of view. While both scientific biology and Uexküll had their respective methods for researching organisms (e.g. genetic analysis or Uexküll's "participatory observation"), it is unclear how we should continue to investigate organisms from a phenomenological set-up. To put it another way, it is unclear whether organisms also show us how we should learn about them. From the phenomenological pretence to develop an interpretation that is more *primordial* than others, I think it remains an open question how we should progress after giving such an interpretation.

For something I would like to further consider, Merleau-Ponty's account of the instituted-instituting relation does not only speak of how something is *comprised*; to this end, an understanding of the constituting-constituted relation would suffice. The idea of institution further introduces a temporal[173] dimension that allows for the possibility of *repetition* in accumulation.[174] Applying this to my discussion of organisms, we can then consider how meaning relations repeat for the organism beyond singular instances of meaning. From the fact that organisms can be solicited or directed by features of the environment (e.g. plants following the direction of sunlight), it is *as if* organism development and behaviour unfold in a pre-

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[173] For Merleau-Ponty, "Time is the very model of institution" (IP, 7).

[174] The example I have in mind to clarify this is the difference between cardinal (1, 2, 3,…) and ordinal (1st, 2nd, 3rd,…) numbers; institution is the establishment of a special kind of accumulation that is *accumulation of the same*, i.e. *repetition.*

established manner (as if the plant *already* had an affinity to sunlight). Here I think Merleau-Ponty's idea of institution can better articulate how this is the case, the idea of institution clarifies how anything can be a "cue" or "signal" for the organism in the first place—that is, signals and cues depend on the idea that organism "deposited with a sense"—without committing us to the problematic narrative of "pre-established" organisms and organism-environment relations.

While I do not mean to suggest my phenomenological interpretation as a contending theory for biological science—as this would already commit us to too much for phenomenology—what I do wish to contribute is a clarification of how we arrive at our scientific theories. Given the nuanced nature of phenomena (indeed, this is why we have competing interpretations of the same facts), I suggest lastly that we should keep an open attitude with regards to what we can learn about organisms.

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