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ORGANISM-ENVIRONMENT INTERACTIONS IN EVOLUTIONARY THEORY

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Supervisor:
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Dissertation presented in partial fulfilment of the requirements for the degree of Doctor of Philosophy

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ABSTRACT

This dissertation concerns the active role of the organism in evolutionary theory. In particular, it concerns how our conception of the relationship between organism and environment, and the nature of natural selection, influences the causal and explanatory role of organismic activity and behavior in evolutionary explanations. The overarching aim is to argue that the behaviors and activities of organisms can serve both as the *explananda* (that which is explained) and the *explanantia* (that which explains) in evolutionary explanations. I attempt to achieve this aim by offering three central arguments.

First, that the organism-environment relation is the ontologically basic unit of biology. A common way of conceiving the relationship between organism and environment is as a duality—as two causally independent systems that overlap through interaction. I think this is a mistake. There cannot be organisms without environments and *vice versa*. They are *codependent* and *codetermined*.

Second, that natural selection is an *ecological* process. By this I mean that natural selection acts primarily on organism-environment interactions. It is only in virtue of organisms interacting with their environments that there can be fitness differences amongst individual organisms in a population. The ecological approach to natural selection also entails that the nature of the system(s) of inheritance involved in the reoccurrence of favorable organism-environment interactions is, in principle, immaterial to the process of selection. It only matters for selection that organism-environment interactions actually do reoccur in subsequent generations.

Third, that niche construction theory—the most well-developed theoretical and conceptual framework for studying how the activities of organisms influences evolutionary dynamics—can be seen as fully a compatible and integrated part of evolutionary theory.

Together, these three arguments constitute an overarching argument. Namely that we both can, and should, take organismic activity and behavior to be crucial explanatory elements in evolutionary theory.

Throughout the dissertation I also show how these three arguments have consequences for other debates in the philosophy of evolutionary theory, such as the nature of evolutionary processes, the structure of selection-based explanations, the validity and utility of the proximate-ultimate distinction, and the nature of teleology in evolutionary systems.

PREFACE

The content of this dissertation is adapted from five journal article manuscripts, two of which have already been accepted for publication. The remaining three are currently at different stages of the peer-review process. The introduction, chapter 2, and the conclusion are not based on article manuscripts, as they are indented to provide context and motivation for all subsequent chapters. While this dissertation has been adapted into a monograph, I have elected to retain the narrative style of the individual journal articles. Each chapter contains an introduction and conclusion and can in principle be read as self-contained arguments in any order the reader might choose. However, I would strongly recommend the reader to begin with the introduction and work through the chapters in the intended order.

I have chosen the particular order of the chapters for narrative and structural reasons. The chapters 2-5 contain arguments concerning what explanatory role organism-environment interactions can play in evolutionary theory in general. Chapters 6-7 focus on the theoretical and conceptual framework of one kind of organism-environment interaction that is argued by many to be of significant explanatory relevance in evolutionary theory—namely *niche construction*. The reason for starting with the general arguments with a broad scope, and later move to the more specific arguments with a narrower scope, is that I regard the arguments of the first few chapters as somewhat of a buttress for the later chapters. Chapter 6 and 7, which deal with niche construction in particular, can be seen as a critical look at one of the many instances in which organism-environment interactions need to be treated as the *explanantia* ("that which explains"), and not only the *explanandum* ("that which is being explained") in different evolutionary outcomes. Thus, it seems reasonable that the arguments for why and how organism-environment interactions can be explanatorily salient in evolutionary theory should preempt the arguments concerning how we should conceptualize the specific instances of such organism-environment interactions captured by niche construction theory.

While the arguments of the first three chapters may be seen as a buttress for the later chapters, they do not have to be. Another consequence of the decision to retain the narrative style of the individual articles is that the argumentation in each chapter can to some degree be evaluated in isolation. In other words, the arguments in each chapter are self-contained and do not rely on premises or conclusions from other chapters. There are pros and cons that follow from having chapters that are argumentatively self-contained. One of the pros, which I myself appreciate the most, is the freedom it gives the reader. Not only can the reader choose the order in which to engage with the material—one can choose to start with the topic that peaks one's interest (or alternatively with what seems least dreadful), by length of the chapter (if that helps in getting through it on an otherwise busy schedule), or simply follow the narrative structure provided—one can also read one chapter, leave it, and return at a later stage without having to re-read prior pages or chapters in order to recollect the argumentative and narrative context of the whole. There are of course drawbacks with the freedom offered by self-contained chapters. There is the possibility that some of the overlapping content, which is necessary for the cohesion of each individual chapter, ends up being repeated on several occasions. On this point I have attempted to strike a balance. On the one hand, I want to keep the narrative and argumentative structure of the journal articles each chapter is based on. On the other hand, I want to avoid tedious repetition and narrative inconsistency. Consequently, I have made efforts to produce a result that reads as a monograph but is composed of self-contained chapters. I hope the reader will construe it as that as well, though some repetition is inevitable.

Finally, the list below provides information of what manuscript each chapter is based on and which journal it is published in or submitted to. As mentioned above Chapters 1, 2, and 8 are not based on journal article manuscripts.

Chapter 3 is based on:	**Aaby**, **Bendik Hellem**. [2021]. The Ecological Dimension of Natural Selection. *Philosophy of Science*. Forthcoming December 2021, Vol. 88(5).

Chapter 4 is based on:	**Aaby**, **Bendik Hellem**. [Status: Revise and Resubmit]. Niche Construction and the Selection of Favorable Interactions. *The British Journal for the Philosophy of Science*.
Chapter 5 is based on:	**Ramsey**, **Grant** & **Aaby**, **Bendik Hellem**. [Status: Revise and Resubmit]. A Structuring-Triggering Interpretation of the Proximate-Ultimate Distinction. *Biology & Philosophy*.
Chapter 6 is based on:	**Aaby**, **Bendik Hellem** & **Ramsey**, **Grant**. [2019]. Three Kinds of Niche Construction. *The British Journal for the Philosophy of Science.* First published online 05 December 2019. doi:axz054
Chapter 7 is based on:	**Aaby**, **Bendik Hellem**. [Status: Revision Submitted]. Niche Construction and Teleology: Organisms as Agents and Contributors in Ecology, Development, and Evolution. *Biology & Philosophy.*

Since two of the chapters are based on coauthored manuscripts, the appropriate self-referential pronoun would be ‘we’. For the sake of narrative cohesion, I have elected to use ‘I’, although I sometimes regard the reader as a conservational partner and use the colloquial ‘we’ and ‘us’ to refer to both myself and the reader. While the opinions and arguments of the original coauthored manuscripts belong equally to my coauthor, I, and I alone, am responsible for any error or shortcomings the reader may discover in the following text.

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Bendik Hellem Aaby
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INTRODUCTION AND OVERVIEW

1.1 Statement of Aim and Purpose

There are three mutually reinforcing arguments that inform this dissertation. The first is an argument that the organism-environment relation is the basic ontological entity in biology. The second is an argument in favor of viewing natural selection as an ecological process primarily concerned with the outcomes of organism-environment interactions. The third is an argument in favor of seeing niche construction theory as a fully compatible and integrated part of evolutionary theory which helps us better understand how organismic activity and behavior influences evolutionary dynamics. These three arguments together can be seen as constituting a single argument in favor of the overarching thesis of the dissertation, namely that organismic activity, behavior, and other developmental processes can serve as both *explanatia* and *explanada* in evolutionary explanations. By arguing that natural selection is an *ecological* process I mean that natural selection primarily acts on the outcomes of organism-environment interactions. Further, by being an ecological process, natural selection will not be directly sensitive to what system of inheritance which is responsible for the reoccurrence of favorable organism-environment interactions in subsequent generations, only that they reoccur. Of course, the fidelity of different systems of inheritance in transmitting the necessary information and resources such that the organism-environment interactions reoccur in subsequent generations might influence the response to and directionality of selection. By adopting an ecological view of natural selection, I argue that we can make room for organismic activity as being the *explanantia* in certain evolutionary events, without needing to revise or extend the theoretical principles or causal framework of evolutionary theory.

The ecological approach to natural selection is motivated by an ontological thesis about the relation between organisms and environments. Organisms and environments are usually taken to be a duality in evolutionary theory. In chapter 2 I suggest that such a conception is at best an epistemological heuristic or abstraction, at worst a mistake. Instead, I argue that organisms and environments are inextricably linked—codependent and codetermined. Environments cannot exist without organisms inhabiting them, and conversely, there cannot be organisms without environments. Further, the properties of organisms and environments are constrained by each other. The properties of an organism constrain what parts of the external surroundings that are environmental factors. Likewise environmental factors constrain the possible phenotypes organisms can manifest. The codependency and codetermination between organism and environment serve as the premises of the ontological thesis that the organism-environment relation is the basic entity in biology. Organisms and environments are thus the relata of this basic entity, and exist independently only as abstractions. The fundamentality of the organism-environment relation points to a causal parity between environmental factors and organismic activity in shaping the selective environment and consequently the action of selection on populations of individuals. This contrasts with externalism—the view that selection pressures are formed by environmental factors alone and that natural selection is an environmental process—and opens up the possibility for organisms to play an active role in evolutionary theory.

1.2 The Active Role of the Organism in Evolutionary Theory

The antagonist of this dissertation could be seen as the asymmetrically externalist approach to evolutionary explanations. This approach embodies the dualistic view of the organism-environment relationship most vividly. As we shall see in greater detail in the subsequent chapters, on the asymmetrically externalist view, the organism and environment are treated two separate causal systems that sometimes overlap through interaction. The organic system (i.e., the organism) develops according to its own internal principles (usually understood as an unfolding of a genetic program or as a series of gene expressions). Similarly, the environment is conceived as its own autonomous causal system, and its dynamics are governed by principles internal to the system. The relationship between the organism and environment is seen as one in which the organisms must solve preconfigured environmental problems in order to survive. These preconfigured environmental problems consequently act as selection pressures, making natural selection a purely environmental process. Thus, changes to the distributions of phenotypes in a population is explained in virtue of how well different *genotypes* fare in developing phenotypes that can solve the problems posed by the environment, relative to the other genotypes of the population. Since genotypes carry a predetermined "code" or "program" for developing phenotypes, and since any phenotypic features which are acquired during development do not get transmitted to the next generation, it is only the prior action of selection on a population of different genotypes and chance mutations that can produce phenotypes which solve the problems posed by the environment. Thus, through chance and environmental filtration (i.e., natural selection) populations evolve to become better at solving environmental problems. This is the externalist part. The asymmetry stems from the lack of influence organisms have on the configurations of the environment. The environmental configurations are seen as fully explainable in terms of the dynamics internal to the environmental system itself.

Thus, on an asymmetrically externalist approach to evolutionary explanations, organismic activity and behavior can only be *explanada* (that which is being explained). Since natural selection is conceived as an environmental process that eliminates non-beneficial phenotypes and retains beneficial ones in virtue of genetically inherited parent-offspring phenotypic similarity, the activities and behaviors of organisms are conceived to be largely (though not exclusively) determined by genetic predispositions. The asymmetrically externalist approach is thus skeptical about allowing the activities of organisms that are not the result of genotypic variation to play the role of *explanantia*. The reason is that it comes uncomfortably close to allowing Lamarckian evolution through acquired characteristics. As such, the organism (or phenotype) is treated simply as the object of—and not a subject or agent in—evolutionary processes. The Lamarckian apprehension the asymmetrical externalist may feel is due to the false idea of organism and environments being a duality. If we instead adopt the view in which the organism-environment relation is the fundamental entity in biology, there is room to allow organisms to play an active role as subjects and agents in evolutionary theory.

1.3 Inheritance, Reoccurrence, and the Levels of Selection

Before I provide an overview of the contents of the dissertation, I would like to address two debates which happen at "the backstage" of the dissertation. In chapter 3 and 4, I argue that the only thing that matters for (directional) selection is that the fitness enhancing aspect of a phenotype *reoccurs* in subsequent generations. I also argue that natural selection primarily acts on the outcomes of individual-level organism-environment interactions in a population. However, a general discussion of the debates concerning *multilevel selection* and the role of *soft inheritance* in evolutionary theory is not really provided within any of the subsequent chapters, so I will deal with those briefly here.

Let me begin with multilevel selection. At first glance, viewing natural selection as an ecological process which primarily acts on organism-environment interactions might seem to restrict selection to the level of the individual. However, it seems clear that both conceptually (e.g., Hamilton 1964a, 1964b) and empirically (e.g., Wade 1977), such a restriction of the objects of selection is false. There are plenty of instances in which selection acts on entities that are either above or below the level of individuals. The evolution of eusociality in insects, for example, seems to be a clear instance in which it is the group (i.e., the colony) that undergoes selection and not the individuals that make up that colony, as most of them lack the ability to reproduce. In that case, there is selection on group-environment interactions. Natural selection still acts on the outcomes of organism-interactions, it is just that in some cases organisms may interact with their environment *as* a group, or at least for the sake of other group members' inclusive fitness (i.e., kin selection).

Selection may also act on entities below the level of individual organism-environment interactions. In cases of intragenomic conflict, for example, some genes may replicate and proliferate at the detriment of other genes within a shared genomic environment, i.e., within the same genome (Burt and Trivers 2006). The proliferation and replication of such genes might even result in detrimental effects on the phenotype. An example of this can be seen in the maintenance of homozygous sterility in the house mouse (*Mus musculus*) due to meiotic drive (the distortion of segregation causing an allele to have a greater than 50% chance of being transmitted). In male a heterozygous (*Tt*, *tT*) the *t* allele kills the sperm which carry the normal T allele during segregation, resulting in 90% of male sperm carrying the *t* allele. However, embryos that are *tt* homozygous either die or become sterile. Despite the obvious disadvantage at the individual-level, the meiotic drive of the *t* allele is so strong that it reaches high frequency in many populations of house mice (Futuyma and Kirkpatrick 2017). There is thus selection for the *t* allele at the level of the gene. I do not mean to dispute this. However, it is important to note that in such cases natural selection doesn't cease to act on individual organism-environment interactions. It just that the genic selection *for* the *t* allele is stronger than the selection *against* it by the elimination of mice that are *tt* homozygous at the level of individual organism-environment interactions.

Thus, whenever I state that natural selection acts on the outcomes of individual-level organism-environment interactions, without adding the qualification "primarily", this should not be thought to indicate that I think selection at levels other than the individual is impossible. It clearly happens. However, I still think that selection at the level of individual organism-environment interactions is the rule. Selection happening at other levels than the individual can be seen as (special) instances in which selection is stronger at those levels than that of the individual (e.g., in eusocial- and social evolution, intragenomic conflict, etc.).

Moving to the question of *soft inheritance*. The reason why I have chosen to use the word 'reoccurrence' and not 'inheritance' is that, first, something can be inherited and not expressed in the subsequent generations. This would constitute an instance in which there is heredity and but selection stops (it could still be inherited, but not in virtue of being selected *for*, e.g., cryptic genetic variation). Second, and more importantly, the notion of reoccurrence is supposed to be relatively neutral to the question of the role of *soft inheritance* (i.e., non-genetic systems of inheritance) in evolutionary theory. For me, the significance of different systems of inheritance is both context sensitive and contingent. It cannot, and indeed should not, be generalized across all organisms. Although I am inclined to think that the genetic system of inheritance is in one sense (at least) causally privileged. It is, after all, the system of inheritance that provides the necessary information such that the capacity for autopoiesis can reoccur in subsequent generations, which makes it the central system of inheritance in evolutionary theory. However, this is not a conceptual truth, but a contingent fact. There could have been a different system of inheritance with different properties that stood at the center of evolutionary theory. Further, systems of inheritance can themselves evolve. This is particularly true of soft inheritance systems, which makes the significance of soft inheritance in the reoccurrence of certain organism-environment interactions dependent on the capacities of the organism in transmitting the relevant resources and information to its offspring.

I will therefore limit my arguments to the conceptual possibility that several systems of inheritance can be involved in the transmission of developmental and environmental resources and information that makes certain organism-environment reoccur. This possibility is consistent with a general definition of evolution as "inherited change in the properties of groups of organisms over the course of generations" (Futuyma and Kirkpatrick, 2017, 7). The way I see it, what system or systems of inheritance that makes the changed properties of organisms reoccur over the course of generations is not a conceptual question for evolutionary theory to deal with, but rather an empirical question.

If one so chooses, one could extrapolate from the empirical evidence to formulate a *particular* and *contingent* theory of biological evolution based on particular systems of inheritance. The most famous example of this is the neo-Darwinian theory of evolution, which takes biological evolution to consist solely in changes in allele frequencies in populations of organisms (e.g., Scott-Phillips 2014) and exclude other systems of inheritance by appealing to the Weismann barrier—hereditary information moves *only* from germline cells to somatic cells. Thus, changes (e.g., mutations) to somatic cells during development are not transmitted to subsequent generations. Another example of a specific and contingent formulation of evolutionary theory based on particular systems of inheritance is the gene-culture coevolution theory of human/hominid evolution in which two, partially interacting, systems of inheritance—cultural and genetic—are at play (e.g., Durham 1991; Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981). As a final example, take the developmental systems approach to evolution (e.g., Oyama 2000; Griffiths and Gray 1994, 2001). On this view there is causal parity between a multitude of systems of inheritance and other informational and causal sources responsible for the reoccurrence of the developmental system over generations.

What is common to all of these is that they are all *contingent* and *specific instantiations* of the theory of Darwinian evolution (Dickins and Dickins 2018). They agree (mostly) on the conceptual content of Darwinian evolutionary theory (differential reproduction and common descent), but disagree on the empirical facts concerning how that theory is reified in the natural world around us. Thus, the validity of such theories is an empirical question and not a conceptual matter—barring logical and conceptual inconsistencies.

Conceptually, biological evolution does not need to be as restricted some of these theories suggest, nor does it have to be as inclusive. My arguments to make room for organismic activity, behavior, and development in serving an explanatory role in evolutionary explanations is not limited to a specific instantiation of evolutionary theory. Though my arguments are clearly sometimes incompatible with some of these specific theories of evolution (e.g., the neo-Darwinian theory of evolution). I wish neither to deemphasize or overemphasize the causal role of soft inheritance nor the importance of hard inertance in evolutionary theory *in general*. As biological systems evolve and their capacities change, so does the evolutionary process. Few would deny the importance of cultural inheritance in the developmental trajectory of a human being (e.g., Tomasello 2019). The koala (*Phascolarctos cinereus*) inherits a bacterial culture through the consumption of maternal faecal pap early in development in order to be able to transition from a diet of milk to a diet eucalyptus leaves. This diet only provides enough calories to sustain a koala by the leaves being fermented in their hindgut, something which the bacterial cultures inherited from the maternal feacal pap facilitates (Tyndale-Biscoe 2005). Clearly, stating the importance of the causal factors of development and of different systems of inheritance *in general* is at best an oversimplification and heuristic strategy, at worst, poor scholarship.

Thus, while the reader might see an affinity between the arguments presented in this dissertation with the central theses of the developmental systems approach to evolution, there is an important difference. My approach does not commit to the causal parity of certain developmental and hereditary mechanisms in evolutionary theory as the developmental systems approach does. As such, I would say that my approach shares more with Mayr's phenotypic view of biological evolution:

> Evolution deals with phenotypes of individuals, with populations, with species; it is not "a change in gene frequencies." The two most important units in

> evolution are the individual, the principal object of selection, and the population, the stage of diversifying evolution. (Mayr 2001, xiv-xv)

I would, however, make a slight alteration to his definition:

> Evolution deals with phenotypes of individuals, with populations, with species; it is not "a change in gene frequencies." The two most important units in evolution are the *individual organism-environment interactions*, the principal object of selection, and the *population of organism-environment relationships*, the stage of diversifying evolution. (Paraphrased from Mayr 2001, xiv-xv)

The phenotype includes the biochemical, physiological, morphological, and behavioral characteristics expressed in an organism during its lifetime (e.g., Futuyma and Kirkpatick 2017, G-13). However, as I will argue below, the phenotype is only an object of selection in virtue of its relation to environmental factors and in virtue of being a member of a population of similar, but not identical, competing phenotypes and their relation to environmental factors. Thus, the fundamental objects of selection are organism-environment interactions and what evolves are populations of similar, but not identical, kinds of organism-environment interactions.

I have attempted to construct my arguments in such a way that they are amenable to most specific theories of evolution. However, some of these specific theories of evolution suit my approach better than others (e.g., organism-centered approaches to evolution[1]). I wish, however, to emphasize that I do not think that other approaches, such as the "gene-centered" neo-Darwinian account of evolution as changes to allele frequencies in a population are necessarily *false*. I just think that they do not cover *all* biological evolution that we can observe in the endless forms of life in our natural world.

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[1] Strictly speaking, I would argue that a more appropriate characterization of the "organism-centered" approach to evolution would be as an "organism-environment interaction-centered" approach to evolution. As we shall see in chapter 2, I hold that neither organisms nor environments can be understood in isolation, expect as an abstraction from the more fundamental organism-environment relationship. This view is similar to many of the proponents of "organism-centered" or "ecological" approaches to evolution (e.g., West-Eberhard 2003; Lewontin 1983a, 1983b; Levins and Lewontin 1985; Sultan 2015; Walsh 2013, 2015, 2021).

I hope to have avoided undue partisanship and would like the reader to think of the content of this dissertation as being a contribution to a more pluralistic attitude in evolutionary theory in which evolution itself is seen a process that can evolve and thus open up new ways for biological evolution to obtain. Or, if the reader is inclined, even as a contribution to the debate on general or universal Darwinism (e.g., Dawkins 1983; Dennett 1995).

1.4 Overview of the Content

The rest of the dissertation consists of six argumentatively independent, but mutually reinforcing, chapters and a conclusion which ties those arguments together.

In chapter 2, I argue that organisms and environments are *codetermined* and *codependent*. By this I mean that organisms and environments cannot exist separately and that they are mutually constraining. This leads to adaptations being defined as a property of an organism that only can exist in virtue standing in a functional relationship to environmental factors. Likewise, the ingredients of the process of natural selection—the selection pressures—are formed out of the relationships between environmental factors and properties of the organisms in a population. This chapter can be seen as providing the metaphysical and conceptual backdrop of the dissertation. While not always explicitly expressed throughout the rest of the dissertation, the view that the fundamental unit of biology is the organism-environment relation, that the principal objects of selection are (the outcomes of) organism-environment interactions, and that the principal unit of evolution are populations of organism-environment relationships, informs all the discussions in the subsequent chapters.

In chapter 3 I argue for an ecological approach to natural selection. By this I mean that we should view natural selection as acting primarily on the outcomes of the interactions organisms have with their environment that influences their relative reproductive output. Natural selection will not be (directly) sensitive to which particular system of inheritance ensures the reoccurrences of organism-environment interactions over generations, as long as the they do reoccur. I end by illustrating some of the consequences of taking natural selection to be fundamentally an ecological process by showing how natural selection relates to other processes that influence evolutionary outcomes, such as niche construction and the Baldwin effect.

In chapter 4 I continue the argument from chapter 3. I start by going through the asymmetrically externalist approach to evolutionary explanations in more detail. As we have seen, externalist approaches conceptualize the environment as the causal agent behind natural selection. According to proponents of niche construction theory (NCT), this view omits the active role of the organism. They argue that an additional evolutionary process, niche construction, is in play in biological evolution, and argue that evolutionary explanations often need an *interactionist* structure. NCT argue for interactionist explanations from the view that natural selection and niche constriction are antiparallel processes. I argue that such a conception of the relationship between natural selection and niche construction actually reifies natural selection as a purely environmental process, which it is not. I end by showing how the ecological approach to natural selection can help show how niche construction is one of many processes that might influence the outcomes of organism-environment interactions and consequently be acted on by natural selection. This allows for interactionist explanations without conceiving of niche construction and natural selection as antiparallel processes.

In chapter 5 I look at some recent attempts to undermine the distinction between proximate and ultimate causes and explanations due to Mayr (1961). The opponents of the proximate-ultimate distinction argue that it excludes individual-level and developmental causes from having causal efficacy in evolution and consequently from being explanatorily relevant. I examine two of these arguments; the causal parity argument (or the argument from constructive development) and the causal incompleteness argument (or the argument from reciprocal causation). Both of these arguments rely on an assumption of identity between proximate and developmental causes, and ultimate and evolutionary causes. Neither of these arguments hold—even if we grant the identity assumption. I also argue that both the arguments and the identity assumption stem from an uncharitable reading of Mayr. I offer an alternative, more charitable, reading of Mayr showing how he himself argued that individual-level behavioral processes could initiate evolutionary change. At the end of the chapter, I offer an alternative interpretation of the proximate-ultimate distinction based on Dretske's (1988) distinction between structuring and triggering causes. On this view proximate causes are those that trigger individual-level developmental processes and ecological interactions and ultimate causes are those that structure population-level processes or otherwise influence population level outcomes. This interpretation allows individual-level processes, such as niche construction and phenotypic plasticity to be ultimate causes, as long as they structure the action of population-level processes or otherwise influence population-level outcomes.

In chapter 6 I move on to niche construction theory in particular. I argue that if niche construction concerns how organisms can change selection pressures by altering the feature-factor relationship between themselves and their environment, then there are three fundamental ways in which organisms can engage in niche construction: through constitutive, relational, and external niche construction. This tripartite categorization is a reconceptualization of the canonical categorization in niche construction theory. On the canonical account, niche construction occurs through two fundamental kinds of organism-environment interaction: environmental perturbation and relocation. I motivate my reconceptualization by showing some examples of organismic activities that fall outside of the canonical categorization of niche construction, but nonetheless should be included. I conclude the chapter by discussing two objections to niche construction in general and show how the tripartite categorization can help undercut those.

In chapter 7 I argue that organisms can be active subjects in their own development, ecology, and evolution through niche construction in virtue of two different roles: as *agents* and as *contributors*. I flesh out this difference in terms of purposiveness. Organisms are agents when the niche constructing effects are a result of a *goal-directed behavior*, while organisms are contributors when the niche constructing effects do *not* arise from a goal to perform the constructive activity. Because this distinction is based on teleology, it falls outside the causal-mechanistic categorization introduced in chapter 6. I illustrate the difference with two examples, bacteria creating novel niches through excreting energy-rich metabolites (San Roman and Wager 2018) and plants altering leaf-morphology in order to improve their capacity for receiving light (Sultan 2015). The difference between agential and contributional niche construction is important for understanding the different ways organisms can actively participate in development, ecology, and evolution. Additionally, the distinction can increase our understanding of how the capacity of agency is distributed across the tree of life and how agency influences developmental and evolutionary processes.

Chapter 8 is the conclusion. Here I draw together the arguments from the preceding chapters to show how they together can be seen as an overarching argument for the validity and utility of treating organism as active subjects and agents in evolutionary theory. This allows organismic activity and behavior to be both the *explanantia* and the *explananda* in evolutionary explanations. At the very end I offer a short epilogue on what I take to be the most controversial consequence of the dissertation, namely the introduction of non-reductive teleological explanations and the possibility of goal-directed alterations to selection pressures through organismic agency.

2

ORGANISMS, ENVIRONMENTS, AND EVOLUTIONARY THEORY

2.1 Introduction

In this chapter I explore the concept of the environment and how it relates to the concept of the organism. The concept of environment plays a significant conceptual and explanatory role in evolutionary theory and is often left unanalyzed. However, as I hope will become clear from this chapter, paying attention to the concept of environment has significant influence on how we view other evolutionary concepts, such as adaptation and natural selection. The common-sense view of the organism and environment is as being a duality in which the environment is seen as its own autonomous causal system which the organism—also its own autonomous causal system—inhabits and interacts with. On such a view, it makes sense to talk of the organism and environment as being separate systems that influence each other through interaction. In other words, the organism and the environment are decoupled (Chiu 2019; Walsh 2021). This is the view which underlies the notion of natural selection being purely an *environmental* process—a process in which preexisting environmental configurations are impinging themselves on the organism such that the organism, in its struggle for existence, must consequently adapt *to* in order to survive and reproduce. It is also what underlies the conception of *empty* niches as being constituted by certain environmental configurations ready for potential organisms to *fill* (or adapt *into*). I think this view is misguided and leads to some unwanted consequences. The unwanted consequences will be elaborated in the subsequent chapters in the discussions on the asymmetrically externalist approach to natural selection and adaptation. In this chapter, I will argue in favor of a view in which the organism-environment duality is an abstraction from an ontologically privileged entity—the organism-environment relationship. The organism and the environment are *codependent* and *codetermined*. There cannot be organisms without environments, and there cannot be environments without organisms. The characteristics of the organisms constrains the possible physical factors that can constitute environmental factors, and the environment constrains the possible phenotypes of organisms. The arguments and views presented in this chapter can be seen as motivating the arguments in the subsequent chapters of the dissertation.

2.2 The Environment and its Organism

Organisms and environments are inextricably linked. For organisms to survive and reproduce they need to interact with their environments. Conversely, environments are defined in relation to the organisms that inhabit them. We sometimes refer informally to *the* environment, by which we might mean something like the totality of the natural world, often excluding or in contrast to, human beings and artefacts. This is usually the sense in play when conducting general discussions on what is good or bad for *the* environment, or in relation to whether something is considered *natural* or *unnatural*. We also talk about environments in another, more abstract, sense. As denoting the external surroundings, influences, and conditions of something or someone. We often use it in this sense when describing the people and objects that surround and influence us in specific contexts, such as when someone is talking about how wonderful the work *environment* has become under new HR management. This abstract sense is reflected in its etymology. The word 'environment' is derived from the Old French word 'environner' (to surround, to encircle) and the Latin derivational suffix '-ment' (used to transform verbs into a nouns), which together denote something like "the state or action of surrounding or encircling".

In biology, the objects that are surrounded or encircled are organisms. Thus, the singular, informal sense of *the* environment described above is seldom what is meant. The abstract sense of environment is also rarely used unless the discussion takes place wholly at a conceptual level. Rather, the notion of environment as it is used in biology is reified relative to concrete objects. The least concrete class of entities being those that are referred to by concepts like ‘organism’, ‘populations’ or ‘species’. Usually, however, the concept of environment will be qualified to even more concrete objects, to *particular* organisms or species. For example, we often see a qualification like “the environment *of the Kalahari lions*” (*Panthera leo melanochaita*).[2] However, what is included in the environment of the Kalahari lion? Is it just the things which surround and influence them? Both Kalahari lions and human beings are surrounded by the celestial objects in our solar systems, and both are influenced by the gravitational forces of Jupiter. But we would not think Jupiter as being a part of the Kalahari lions’ environment, nor our own environment for that matter. The reason why we would not think of Jupiter’s gravitational forces as being a part of the environment of the Kalahari lions is that it is not something which influences the daily lives of the Kalahari lions *in particular*. While it is true that the gravitational pull of Jupiter has saved Earth from countless potentially devastating asteroid impacts and consequently indirectly contributed to the sequence of events leading up to the extant prides of Kalahari lions, characterizing the Jupiter as a salient environmental factor of these lions’ environment seems misguided. If Jupiter were to suddenly disappear, this would have presumably have devastating effects for all life on earth, and not just the Kalahari lions.

What we are after when describing the environment of the Kalahari lions are the *ecologically relevant* factors. These include abiotic factors such as the scorching temperatures of the Kalahari dunes and the low availability of water, as well as biotic factors, such as the presence prey such as the common eland (*Taurotragus oryx*) or the African crested porcupine (*Hystrix cristata*), and absence of competitor species (Eloff 2016; Peterhans et al. 2019). In other words, what we are after when describing the environment of an organism or a species are the salient environmental factors which

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[2] The Kalahari lions, or lions of the Kalahari, are not a distinct subspecies of lions, but rather a (loosely organized) population of the *Panthera leo melanochaita* located in the Kalahari Desert which itself is a subspecies of lion (*Panthera leo*) found in Southern and East Africa (Kitchener et al. 2017).

that organism or species *interacts* with. Such an interactionist approach can be found in Lewontin's conception of an environment:

> The environment of an organism [or species] is the penumbra of external conditions that are relevant to it because it has effective interactions with those aspects of the outer world. (Lewontin 2000, 48-49)

This is an interactionist understanding of the environment. The reason for opting for a more specific definition of environment—one in which only the environmental factors that the organism causally interacts with are considered parts of its environment—is to help in both delineating and operationalizing the concept of environment as it is applied to specific organisms, as well as contrasting between different kinds of organisms and their respective environments. Thus, when we talk about "the environment of the Kalahari lion" we are expected to refer to the set of conditions which influence the lives of a specific population of lions in a specific region, and not conditions that apply to all organisms, or even large groups of organisms (e.g., terrestrial mammals), such as the gravitational pull of Jupiter alluded to above or other general physical conditions that apply to large groups of organisms across many different ecosystems.

2.3 Ecological and Evolutionary Environments

However, simply pointing out what the external factors an organism causally interacts with is still not entirely what we are after when we characterize an organism's environment. If the environmental factor that the organism interacts with has no bearing on its fitness or ecological lifestyle, it is usually not considered an important environmental factor in the ecological and evolutionary environment of the organism. For example, it might be completely inconsequential to a city-dwelling feral pigeon (*Columba livia domestica*) whether the surface where it forages for food is made of tarmac, concrete, cobblestone, or wood. If the foraging behavior is similar across the different surfaces, and the results of the foraging behaviors are similar on average for each surface, then we do not need to specify the material out of which the surface where foodstuffs are located is made when characterizing the feral pigeon's environment.

On the other hand, had there been a difference in the foraging behavior across different surfaces we would most likely include a reference to the surface in our description of the feral pigeon's environment. If, for example, it turned out that cobblestone streets are more likely to retain foodstuffs in stationary locations over longer periods of time relative to other surface materials such as tarmac or concrete where the foodstuffs are moved around more frequently by wind or people, then we might see a difference in behavior in terms of optimal foraging behavior relative to surface material. This could manifest as a benefit of staying on the ground in areas with cobblestone surfaces to quickly access food that is dropped. In areas where the surfaces are made of tarmac or concrete, the optimal foraging condition might consist in staying on higher ground at a vantage point in order to observe where foodstuffs tend to end up after being moved around by wind, people, or other factors. Such a difference in foraging strategies relative to surface material might result in behavioral differences between feral pigeons that primarily forage in the areas of a city that are covered in cobblestone and those that primarily forage in areas with smoother tarmac or concrete surfaces. The cobblestone-foraging pigeon might benefit from a decreased flight-response, and thus tolerate a closer proximity of humans and their companion animals. The tarmac and concrete-foraging pigeons, on the other hand, might benefit from better visual acuity in spotting foodstuffs from a vantage point.

Whether or not the surface material of the foraging arena of the pigeon should be considered a part of its environment thus turns out not to be a clear-cut question of whether the pigeon interacts with it. Rather it turns out to be an empirical and pragmatic question which we need to establish by looking at the behavior, morphology, and physiology of the pigeon, especially in relation to environmental factors that we want to establish as either being a salient or insignificant environmental factor of the feral pigeon's environment.

This might strike some as an abhorrent conclusion. Surely environmental factors are not established by the whim of biologists, but rather are real and mind-independent features of the world. That is of course true. Few would argue that unless a biologist deemed an environmental factor salient for an organism, the factor would not be part of the organism's environment. However, that is not the point of claiming that the factors which are to be considered part of different organisms' environments is an empirical and pragmatic question. It is meant to highlight that the concept of 'environment' is supposed to play a special role when it is utilized in the setting of describing the ecology, development, or evolution of particular organisms. In these contexts, the concept of environment denotes the sets of external factors with which we can describe, explain, and even predict the features of organisms.[3] In an attempt to clarify the different senses of ‘environment’, Brandon (1990) and Antonovics et al. (1988) offer three different ways the concept is used in ecology and evolutionary theory.

External environment: The sum of all measurable factors, both biotic and abiotic, external to the organism.

Ecological environment: The factors of the external environment that affect individual organisms’ contribution to population growth (i.e., survival and reproduction).

Selective environment: The factors of the ecological environment that affect realized *relative* fitness of different individuals in a population.

These three conceptions of environment reflect three different kinds of measurements that are of interest to an ecologist and evolutionary biologist. External environmental factors are measurable independently of an organism. For example, we could measure the concentration of cadmium (Cd) in an inland lake. The external environmental factors do not necessarily influence the organism which we are measuring the environment of. If, for example, we are interested in measuring the environmental factors that are relevant to the common water moss (*Fontinalis antipyretica*), then it might turn out the concentration of cadmium is the wrong factor to measure, as the water moss can absorb a large amount without that having significantly adverse effects on its capacity for survival and reproduction. If, however, we are looking at the environment of the rainbow trout (O*ncorhynchus mykiss*), then the cadmium concentration might be a relevant environmental factor to measure, as cadmium

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[3] This relationship is not necessarily asymmetrical. It is not only environmental factors that explain the presence (or absence) of organismic traits (morphological characters, behaviors, etc.). Sometimes the environmental factors are explained by the activities of organisms, such as Earth’s oxygen rich atmosphere. The reciprocal relationship between organism and environment is a central theme throughout this dissertation and we shall return to it on several occasions.

toxicity may cause severe malady in vertebrates, such as liver disease, renal failure, chronic high blood pressure, nerve and brain damage, as well as affecting birth weight and causing abnormal skeletal development (Hansen et al. 2002; Rodríguez and Mandalunis 2016). Thus, for the rainbow trout, cadmium concentration is both an *external* and an *ecological* environmental factor. Ideally, the measurement provided by an ecological factor would be a measure of a single genotype's (or individual) realized fitness in environments with different cadmium concentrations (this would of course require clones of the genotype for each sample of different cadmium concentrations, as the developmental environment is usually that which affects an organism's realized fitness the most). Regardless of how difficult such measurements are to provide, the idea is that the ecological environment consists of those factors that affect the demographic performance of individuals during their life cycles—it picks out factors that are relevant and significant for the developmental and ecological life history of the organism.

The final sense of environment is the *selective* environment. The selective environment is measured by the realized relative fitness of a population of different individuals (or different *genotypes* in Brandon 1990). Thus, *selective* environmental factors are those that contribute to the differential reproduction of types within a population.[4] For example, a population of interbreeding rainbow trout inhabiting an inland lake can be said to share a common selective environment. If that lake happens to have a high concentration of cadmium, this might produce a selection pressure for an insectivorous and not a piscivorous diet, if, say, insects are less prone to bioaccumulation of cadmium than small fish. In such a case, the rainbow trout that have a primarily piscivorous diet will on average accumulate more cadmium which confer severe deleterious effects and fitness disadvantages. Thus, the concentration of cadmium is both an external, ecological, and selective environmental factor in the environment of (that population of) rainbow trout.

All three different senses are relevant for the ecologist and evolutionary biologist. Ideally, however, they will only need to care about the ecological and

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[4] A common selective environment can only be shared by a population of competing individuals. Thus, even though both the porpoise and dolphin experience selection pressures favoring a hydrodynamic morphology, this is only a selection pressure which happens to feature in both species' selective environments.

selective environments of organisms. As we learn more about an organism's physiology and ecology, we learn what factors of that organism's external environment are also factors of its ecological environment and the population's selective environment.

Thus, when using the concept of environment in explaining biological phenomena, we usually try to explain a relationship between an environmental factor and a feature of an organism, population, or species. The feature of the organism is usually a trait (a specific characteristic of an organism's phenotype), or cluster of traits. The relationships between environmental factors and organismic traits which are of most interests to evolutionary theory are *adaptations*.

2.4 Adaptations and Environments

Some heads might have turned by the last sentence in the preceding paragraph. Did I just claim that an adaptation is a *relationship* between an environmental factor and the trait of an organism? Isn't the adaptation just the trait itself, which belongs to the organism and not to the relationship between the trait and the environmental factors which the trait interacts with? If we look at a general definition of adaptation this does seem to be the case:

> [A]n adaptation is a *property of an organism*, whether a structure, a physiological trait, a behavior, or any other attribute, the possession of which favors the individual in the struggle for existence. We believe that most such traits were acquired by natural selection or, if they arose by chance, their maintenance was favored by selection. (Mayr 2001, 165, my emphasis)

While not everyone will agree with this definition, it is not a very controversial one. It allows for other forces than selection to be the source of an adaptation and essentially takes adaptation to be anything belonging to an organism which is conducive to its survival and reproduction (relative to the other members of its population). My point in claiming that an adaptation is a relationship between a trait (or cluster of traits) and environmental factors is rather that without a characterization of this relationship, we lack an explanation of *why* and *how* the trait can be acquired and/or maintained by natural selection. The metaphor of a lock and key is often used when talking about adaptation and can help illustrate my point. Think of the organism as the key and the environmental factors as the lock. A key with the appropriate notches, ridges, and teeth that open the lock—the organisms that with the traits that best solve (or dissolve) the environmental problems—are replicated and give rise to a new generation of keys with similar (but not identical) notches, ridges, teeth, tips, and shoulders. Over time the lock might change, and the keys follow suit. The keys can follow suit because they are a population of similar, but not identical, keys which were created on the basis of a key that opened the lock at an earlier stage. Of course, if the lock changes too abruptly or if the replication process goes wrong, there might not be any keys which can open the lock in a particular generation of keys. Such cases might lead to the lock staying closed indefinitely—or in the case of natural populations, extinction. This metaphor describes the basic story of adaptations as a product of evolution by natural selection.

The reason for bringing it up in this context is to be able think about a properties and relationships which are analogous to those in the case of adaptations without needing to worry too much about the complexities of biological phenomena. I said above that I think adaptations are relationships between the traits of organisms and environmental factors. However, a standard characterization of what an adaptation is takes it to be a property of an organism acquired and/or maintained by natural selection. Are these mutually exclusive approaches to the concept of an adaptation, or are they compatible? If we look at an analogous situation from the key and lock metaphor, I think we can see that an adaptation could be, and in fact is, both a relation between traits and environmental factors, as well as a property of an organism.

If I ask what a key is, an appropriate answer in many instances would be something like “a small piece of metal with a particular shape that fits a lock”. It could also be a series of numerals or characters, such as a pin code or password. That depends on the lock. Let’s now imagine that I have fashioned a metal object that looks like a key. It is a piece of metal with a head, shoulder, blade, and tip. The blade has notches, ridges, and teeth. In other words, it has all the features of a standard metal key, except it doesn’t belong to a lock. Is this piece of metal a key? I am inclined to say no. It may look like a typical key, but since there is no accompanying lock which it opens, it does not count as a key. Thus, for a piece of metal to have the *property* of being a key, it must stand in a special relationship to something else, namely a lock, and that relationship must be one in which the key opens the lock. The importance of the relationship between the key and the lock becomes even more clear if we think of all potential things that can be keys and locks. If the sequence of numbers '1234' is the correct combination to my bicycle lock, it could be said to be the key to that lock—and that is not even a concrete object. The key for opening your phone might be a scan of your face or your fingerprint. Is then, "being a key", a property attributable to your face? And if I do not own a phone with facial recognition technology, does my face lack that property? Perhaps it is dispositional, and my face could potentially be a key? Whether or not my face has the property of, or has the disposition for, "being a key" is not a question that really make sense unless we also specify what lock it is supposed to be a key *for*. There are a lot of things that could be potentially be keys, especially now that we have digital locks. In fact, the kinds of locks there are limits the possibility space for what kind of keys we can have. Symbolic locks allow abstract objects to be keys. Cameras, microphones, and scanners allow faces, fingerprints, QR-codes, and sounds (to name a few) to serve the same purpose. It is in virtue of the *relationship* between the property-bearing object and the lock that the object can be said to be a key.[5]

Is it the same way with adaptations? I think so. While an adaptation may well be a property only attributable to an organism, the property itself is only attributable insofar as it is conducive to the organism's survival and reproduction. Surviving and reproducing are developmental and ecological challenges, it essentially boils down to the capacity for environmental interaction. An adaptation could then be said to be a property of an organism, but only in virtue of standing in a functional relationship to specific environmental factors and thereby enabling certain interactions. So, let me offer a slightly modified version Mayr's formulation of adaptation:

> An adaptation is a property of an organism, whether a structure, a physiological trait, a behavior, or any other attribute, which it possesses in virtue of that attribute being involved in environmental interactions that favors the individual in the struggle for existence. We believe that such traits were acquired by natural selection or, if they arose by chance or through other means, their maintenance was, is, or will be favored by selection. (Paraphrased from Mayr 2001, 165)

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[5] Conversely, for something to be a lock there need to be something which is a means to open it.

This formulation is not very different from Mayr's original one. There are three alterations I want to touch on which are especially salient for the rest of this dissertation. First, I think adaptations cannot exists in an organism without standing in a special functional relationship with an actual environmental factor or factors which enables certain organism-environment interactions. Second, while I agree that an adaptation needs to be favored by natural selection, I think even more caution is warranted with the potential sources of adaptations. I do not think adaptations are acquired exclusively through either natural selection or by chance but can originate through other means as well. Perhaps especially salient sources of adaptation are processes like plasticity, learning, or behavioral innovation. Of course, the general capacity of an organism to exhibit phenotypic plasticity, learning, or behavioral innovation might be said to be what counts as the adaptation in such cases, and not the actual behaviors or structures that result from them. However, just as a key without a lock isn't really a key, so it is with processes such as learning, plasticity, or behavioral innovation. These are not really adaptations unless they are related to an actual environmental factor. Thus, taking processes such as learning, plasticity, and behavioral innovation to be adaptations in themselves might be slightly misleading. Rather we should look at them as capacities for adaptability. It is only in virtue of responding to actual environmental challenges (and consequently in producing adaptations) that such processes can be acted on by natural selection. If the capacity to learn is not manifested in an actual ecological episode, but rather a silent disposition existing merely as a potential for learning, then it is will be unavailable to natural selection. The inherent adaptability of such processes is not what is acted on by natural selection, it is rather the actual adaptable responses which these processes produce in a given environmental context. However, if there is a lot of environmental heterogeneity for the organism to deal with, then relatively open-ended responses might be beneficial, while if the environment is relatively homogenous and stable, fixed responses might be more beneficial. So, through the action of natural selection over generations, the capacity for adaptable responses (i.e., adaptability) might by modulated, but this modulation happens in virtue of processes like plasticity, learning, and behavioral innovation producing *actual* adaptive (or maladaptive) responses in relation to *actual* environmental factors. If we call a general capacity for plasticity an adaptation, we also owe a characterization of the ecological setting in which such a capacity will be favored by natural selection. Unless the ecological setting is specified, such a feature of the organism cannot really be called an adaption.

Processes such as plasticity, learning, and behavioral innovation can produce novel (often non-genetic) phenotypic variation and can in that sense be non-random sources of adaptations. For example, some Macaws of the Western Amazon have discovered that they can ingest soil from strata exposed in clay licks in order get more salt in their diets. If the soil ingesting behavior gives the Macaws a competitive advantage over the other non-soil-ingesting members of their respective populations,[6] then the soil ingesting behavior will be an adaptation brought about by behavioral innovation (and presumably observational learning allowing the trait to spread in the population). In this case, the capacity for behavioral innovation and observational learning can be seen as non-random sources of adaptation. As long as the soil ingesting behavior reoccurs in succeeding generations, and the behavior consistently produces a fitness advantage, then it will be maintained by natural selection.

This last point brings us to the final point about the paraphrased formulation I wish to discuss. In the paraphrased formulation I hold that an adaptation is a trait that *either has been, is, or will be maintained by natural selection*. The inclusion of ‘will be maintained’ deserves mentioning. I have added this qualification to highlight that natural selection will favor any phenotypic trait that increases an organism’s relative fitness. Whether it is a trait which increases an organism’s relative fitness that occur during its lifetime through plastic responses or whether it is the accumulated product of prior selection on gene frequencies is inconsequential to a selection episode. What is consequential is whether the trait reoccurs in the offspring of the succeeding generation. As in chapter 1, I do not wish to generalize as to the mechanisms of inheritance that are responsible for the reoccurrence of the trait in subsequent generations, as this needs to be established empirically. The relationship between adaptable responses to environmental challenges and natural selection is the topic of the next three chapters and this view will be further elaborated and defended there.

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[6] Soil ingesting behavior from particular strata of exposed soil is exhibited by many different species of Macaw in the Western Amazon. Since the much of the Western Amazon is more than 100 kilometers away from the nearest ocean, salt is a scarce resource (Kaspari et al. 2008). However, salt deposits are found in strata of earlier geological ages. These deposits are exposed and easily available in naturally occurring clay licks which the Macaws have discovered and taken advantage of (Powell et al. 2009).

2.5 Organisms, Environments, and the Fundamentality of Interactions

Just as how different types of locks shape the possibility space of what objects can serve as keys, so do environmental factors and configurations limit the possibility space of what can be or become adaptations. The viscosity of water, for example, greatly limits the possibility space for morphological structures to serve as locomotive adaptations for aquatic organisms. However, the properties of a key also limit the potential shape of a lock. If we, for example, wish our key to portable, then we cannot opt for a lock which uses a crosspiece or a door bar to stay locked. Similarly, features of organisms also influence and shape the possible interactions it can have with its environment. The size of an organism is a great example of something which greatly influence the way in which it can interact with its environment. Being submerged in water, for example, is experienced by small organisms like we would experience being submerged in syrup (Purcell 1977). Thus, physical conditions such as the viscosity of water—which describes a physical state of a liquid and is quite independent of organisms experiencing it—are only environmental factors in virtue of influencing and being experienced by an organism. Thus, thinking of the viscosity water *in general* as an environmental variable is misleading. It results from an epistemological strategy of *decoupling* organism and environment in which the environment and the organisms are treated as two separate causally autonomous interacting systems (e.g., Chiu 2019). The viscosity of water engenders different selection pressures relative to the size of the organism. Relatively large aquatic animals might displace water in order facilitate locomotion. Smaller organisms, lacking the physical prowess to displace water might rather opt for a locomotive strategy in which they penetrate the medium which they are submerged in (Walsh 2015). Thus, while water certainly exists without organisms being submerged in and moving through it, it is not an environmental feature without being related to an organism. This point is made by Lewontin:

> There is no organism without an environment, but there is no environment without an organism. There is a physical world outside of organisms and that world undergoes certain transformations that are autonomous. [...] But the physical world is not an environment, only the circumstances from which environments can be made. (Lewontin 1978, 86)

Treating the environment or the organism as something which exists as autonomous causal systems is thus an epistemological abstraction (e.g., Lewontin 1978, 1983; Chiu 2019; Walsh 2015, 2021). Fundamentally, there is the organism-environment relation. The organism and the environment are the relata of this ontologically basic relation. We can formulate two theses that encapsulate this view:

Codetermination thesis: Organisms and environment *codetermine* each other. The possible phenotypes of organisms are constrained by their environmental factors. Conversely, the physical conditions that count as environmental factors are constrained by the characteristics of phenotypes. Just as a lock determines the possibility space of a key and *vice versa*, so too do organisms determine the possibility space of environmental factors, and environmental factors determine the possibility space of organisms.

Codependency thesis: Organisms and environments are ontologically *codependent*. There cannot be environments without organism and *vice versa*. Treating either the organism or environment as causally autonomous entities is an epistemological abstraction only made possible through conceptualization. The fundamental entities of biology are organism-environment relationships, the fundamental objects of selection are organisms-environment interactions, and the fundamental units of evolution are populations of similar, but not identical, organism-environment relationships.

2.6 Conclusion

In this chapter I have argued that organisms and environments are inextricably linked. Organisms and environments are codependent and codetermine each other. This leads to a view in which the organism-environment relation is the ontologically basic unit of biology. This point has salient consequences for our understanding of central concepts of evolutionary theory. Adaptations, which are commonly defined as features or properties of an organism, usually referred to as traits, cannot be regarded as adaptations unless they stand in a functional relationship to environmental factors. Natural selection, a process commonly seen as acting on the relative fitness differences between different phenotypes in a population, should rather be seen as a process that acts on the outcomes of organism-environment interactions. Evolution, commonly seen as changes to the distribution of different phenotypes (or genotypes) in a population, should rather be seen as changes to the kinds of organism-environment interactions there are in a population.

In the following chapters, we shall see how this view of the organism-environment relation allows organisms to be active subjects and agents, and not merely passive objects, in evolutionary theory.

3

AN ECOLOGICAL APPROACH TO NATURAL SELECTION

3.1 Introduction

The principle of natural selection is the theoretical cornerstone of evolutionary theory. In the philosophy of biology, we can delineate four different, but related, main discussions of this principle; first, on what the sufficient conditions are for its occurrence (e.g., Lewontin 1970; Godfrey-Smith 2009). Second, on the appropriate means of quantifying the influence of natural selection on the distribution of variants in populations over time (e.g., Millstein 2009; Otsuka 2016). Third, on whether selection can be counted as a cause or is more appropriately interpreted as a statistical summary of multiple underlying causes and not a cause of evolution in itself (e.g., Matthen and Ariew 2002; Ramsey 2013a, 2013b; Walsh 2010). Fourth, on whether selection can act on multiple levels and what the relevant units of selection are, and if any of these are privileged (e.g., Williams 1966; Dawkins 1976; Okasha 2006).

Another debate, which is related to all of the aforementioned debates, centers around the metaphysics of evolution. In this debate we can identify two main camps; a molecular, or "gene-centered" metaphysics (e.g., Scott-Phillips et al. 2014; Dawkins

1976, 1982) and an ecological, or "organism-centered" metaphysics (e.g., West-Eberhard 2003; Walsh 2015). Standard textbook evolutionary biology usually has a "molecular" metaphysics, in that the fundamental units of evolution are *gene frequencies* in a population. On an "ecological" metaphysics of evolution, the fundamental unit of evolution are populations of *organisms*.

Walsh (2015), amongst others, has recently argued that the Modern Synthesis misrepresents the metaphysics of evolution by viewing it primarily as a molecular phenomenon, instead of an ecological one. This is largely due to what Walsh calls "the marginalisation of the organism that have taken hold under the Modern Synthesis" (Walsh 2015, *x*). This has been a complaint of many biologists and philosophers over the last decades (e.g., Lewontin 1983a, 1983b, Piaget 1978; Odling-Smee et al. 2003; Oyama 2000; West-Eberhard 2003) and is a central complaint of the proponents of an *extended evolutionary synthesis* (e.g., Pigliucci and Müller 2010). Theoretical and empirical work taking a more ecological or organism-centered approach to understanding evolution and development has also recently gained some traction under the headings of eco-devo (ecological developmental biology) and eco-evo-devo (ecological evolutionary developmental biology). For example, West-Eberhard (2003), Sultan (2015) and Gilbert and Epel (2015) have made a great effort to establish how both evolutionary and developmental trajectories are significantly influenced by, and sometimes crucially dependent on, particular organism-environment interactions.

In this chapter I will look at what an "organism-centered", or "ecological", metaphysics of evolution might do to our understanding of natural selection. I begin from the view that natural selection is primarily an ecological process. By this I mean that natural selection is a process in which organism-environment interactions are what is preferentially selected. Further, natural selection acts on the outcomes of these interactions. This is not a novel view and has been suggested before (Lehrman 1970; Brandon 1990; Rosenberg 1983). However, I will take this a step further and argue that this also means that natural selection is not directly sensitive to which system of inheritance ensures the reoccurrence of such interactions, be it genetic, epigenetic, behavioral, cultural, or symbolic (Oyama 2000; Griffths and Gray 2001; Jablonka and Lamb 2014). Natural selection acts on the outcomes of organism-environment interactions and the frequency and likelihood of their reoccurrence in subsequent generations.

However, this does not mean that I equate the importance of each system of inheritance. A genetic system of inheritance is an important prior condition for there to be other systems of inheritance in most, if not all, organisms. Further, much of morphological and physiological evolution seem to be primarily under genetic control. The point is rather that this happens "unbeknownst" to natural selection. To use some helpful terminology from Sober (1984), we can say that there is selection *for* the ecological interactions that yields highest relative fitness in a population, while there is selection *of* the relevant genes that contribute to those interactions because of the high-fidelity-inheritance properties of the genetic system of inheritance in reliably producing offspring which exhibit similar interactions.

3.2 Selection on Passive Objects by Environmental Filtration

Let's begin by looking in more detail at the "standard" molecular metaphysics of the Modern Synthesis. In most textbooks on evolutionary biology, one is likely to find a definition of evolution as the changes to allele (or gene) frequencies in a population over time (e.g., Futuyma and Kickpatrick 2017). Furthermore, the conditions for evolution by natural selection to occur (e.g., Lewontin 1970); inheritance, variation, and differences in fitness, are often interpreted in a genetic manner. That is, any variation in fitness, which is due to differences in the performance of varying phenotypes in relation to the local (and common) selective environment, is only acted on by natural selection insofar as the genetic underpinning of that variation steadily expresses the relevant phenotype over generations. Since the genetic system of inheritance is privileged, in the sense that without it there would be (in most cases) no organism to be selected for in the first place, it makes perfect sense to define evolution as changes in the frequencies of genes in a population. And from this it easy to conceive of natural selection as being an agent which sorts different genetic variants based on their performance relative to their immediate environment. This rendition of natural selection construes it as an environmental process. The metaphor of a sieve or filtration is often invoked to describe this process (e.g., Sober 1984). Coupled with the view that the only phenotypic variation that matters for biological evolution is that which is the result of genetic variation, such metaphors engender a certain passivity on behalf of the organism. It essentially relegates the action of selection to be realized by certain (stable or changing) environmental configurations. Natural selection acts on those organisms that carry the appropriate genetic material to produce a phenotype that performs best (i.e., highest realized relative fitness) in relation to the relevant environmental configurations. Such a view of evolution by natural selection has been called asymmetrically externalist (Godfrey-Smith 1996).[7] It is asymmetrical in the sense that the configurations of the environment are (presumed to be) explainable solely with reference to factors internal to the environmental system itself. While, on the other hand, the organisms which occupy these environments are explained (in terms of the phylogenetic history leading up to their capacity for occupying the environment) by reference to a combination of changes to the biological system (i.e., changes in the gene frequencies of the lineage(s) leading up to the relevant population) and the environmental configuration which the lineage(s) have experienced over generations. It is externalist in the sense that the environmental configurations are what "trigger" the selection of the phenotype, while the changes to the gene frequencies in the population is a "structuring" cause of the selection event.[8] The role of the organism in such explanations is that of a vehicle (e.g., Dawkins 1978), one that carries certain passengers (genes) to certain destinations (selection events). However, organisms are arguably not just an ensemble of genes, and their activity or behavior might influence their reproductive success and consequently the evolution of their lineage. How does an externalist and molecular (i.e., gene-centered) view of evolution deal with behavior?

Standardly, in behavioral ecology (e.g., Krebs and Davies 1993) and the evolutionary explanations provided by behavioral genetics (e.g., Anholt and Mackay 2010), organismic activity and behavior is treated as any other phenotypic trait. Such a treatment is based on certain assumptions regarding the dispositional properties of genes in relation to behaviors and certain optimality measures (Krebs and Davies 1993). Generally speaking, organisms exhibiting behaviors that increase their fitness are selected for, and the disposition to exhibit the beneficial behavior in subsequent generations is assumed to be under genetic control—and can consequently be treated

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[7] The asymmetrically externalist approach to adaptation and natural selection and its motivation is a central topic of the next chapter and will be treated in more detail there.

[8] The distinction between "structuring" and "triggering" is used by Ramsey (2016) to show how fitness, selection, and drift can be understood as structuring causes of evolution. In chapter 5 I will invoke this distinction show how the proximate-ultimate distinction can allow organismic activities and other individual-level causes to have evolutionary effects (i.e., be ultimate causes in evolutionary explanations).

like any other phenotypic trait. The validity of these assumptions is not under question here. The point here is a conceptual one. It is about how we conceive of the relation between natural selection and the organisms exhibiting the relevant behavior. Let's conduct a simple thought experiment. Imagine an imaginary species of animals like the *tarbutniks* from Avital and Jablonka (2000). The individuals of this species have completely identical and non-changing genetic make-up. In other words, it is a species without genetic variation among the individuals. However, let's assume that they can differ in their behavior, i.e., that there is still phenotypic variation. Some individuals forage fruits to supplement their diet, while others obtain their nutrients from only eating grass. This then leads to the fruit-foraging individuals having a more energy-rich diet, which increases their reproductive output. Let's further imagine that the fruit foraging techniques are passed on vertically through parental guidance (i.e., learning) and that the transmission of this behavior from parent to offspring enjoys a high level of fidelity. If we view natural selection as a process that sorts genetic variation, then there is no response to selection in this scenario. However, this seems wrong. Surely, natural selection still acts on the individuals that forage fruit to supplement their diet if this increases their reproductive output. Thus, there is a response to selection in the population—the number of fruit-foraging individuals increases and fruit-foraging behavior spreads throughout the population.

While in this thought experiment natural selection does not lead to biological/genetic evolution (in the sense that the gene frequencies in the population remain unchanged), natural selection has still occurred. And while some might hold that for natural selection to bring about adaptive *biological/genetic* evolution there must selection amongst different genetic variants in a population (e.g., neo-Darwinians), there is still natural selection amongst the phenotypes of our imagined population.[9] The strength and direction of the selection for the fruit foraging behavior is dependent on the fidelity and transience of the behavioral inheritance system, as well as the relative fitness impact of the beahvior.

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[9] As I argued in the introduction (chapter 1), I think it should still count as biological evolution. While non-genetic biological evolution may be more transient and ephemeral than genetic evolution, there are still changes to the distribution individual *tarubtniks* in a population due to fitness enhancing inherited (viz. reoccurring) properties.

Even though there are no organisms like the *tarbutniks* in the real world and we do not know exactly to what extent difference in behavior and capacity for learning is linked to and/or governed by genetic variation in a population, the point about the natural selection being an ecological process still stands. Natural selection is not directly sensitive to what causes the phenotypic variation available for selection to act on, just the outcome of different interactions between phenotypes and their environments. This is an important consideration for both biologists and philosophers taking a more organism-centered approach. These argue that organisms are not merely passive objects of selection, but active subjects—or agents—in their own evolution (e.g., Lewontin 1983a, 1983b; Odling-Smee 2003; Bateson 2004). Let us now turn to these organism-centered views, and in particular two processes in which the activities of organisms are thought to play an important part in shaping evolutionary dynamics—the Baldwin effect and niche construction.

3.3 Organisms as Agents in Evolutionary Theory

Over the course of the last decades there has been an increasing tension in evolutionary biology, culminating in an overarching debate surrounding whether an extended evolutionary synthesis is needed (Müller and Pigliucci 2010, Laland et al. 2014a; Wray et al. 2014). A central part of this debate concerns the role that behavior, and organismic activity more generally, has on evolutionary dynamics. The question of how the activities and behaviors of organisms can alter the action of natural selection has a long history. It could, arguably, be said to date all the way back to Lamarck (Avital and Jablonka 2000). Alternatively, we can trace it back to the introduction of organic selection (also called the Baldwin effect) in the late 19th century (Baldwin 1896a, 1896b; Morgan 1896; Osborn 1896). Organic selection refers to an evolutionary process that can turn acquired characters into congenital ones. More precisely, it refers to a three-step process; first, organisms can through their interactions with the environment systematically produce behavioral, morphological, or physiological modifications that are not hereditary, but increase the fitness of the organism that acquires them. Second, there is genetic variation in the population producing hereditary characters similar to characters that are acquired by the organisms through their environmental interactions. Third, this genetic variation is acted on by natural selection and subsequently spread in the population over the course of generations. The character was initially individually *acquired*, but is in time turned into a *hereditary* character (Simpson 1953). This process has recently garnered more attention in evolutionary biology. In the works of the late Patrick Bateson (2004, 2017a, 2017b; Bateson and Gluckman 2011) this process is revisited in light of what we have learned about social learning, transmission, and non-genetic systems of inheritance over the last decades. Bateson refers to the Baldwin effect as the *adaptability driver* (Bateson 2017a). By this he means that, more often than what we may initially have thought, behavioral plasticity (behavior which is the result of stimuli or interactions with the environment, and not determined by genetic factors) is actually crucial in initiating adaptive responses to environmental challenges.[10]

Another example of organismic activity altering evolutionary dynamics can be seen in niche construction theory (Odling-Smee 2003). Niche construction refers to cases where organisms modify selection pressures by actively altering their environment or their relationship to it. The paradigmatic example being the beaver, which significantly alters the local environment by building a dam, and consequently altering the selective environment it experiences. Both the Baldwin effect and niche construction are central elements in the discussion of an extended evolutionary synthesis. The argument for an extended synthesis from niche construction theory is that in viewing organisms as merely passive objects that are filtered by natural selection we neglect the active role of the organism in its evolution (Odling-Smee 2003). They see niche construction as an evolutionary process whereby the activities of organisms counter or direct the action of natural selection. Consequently, they argue that niche construction should be seen as a potentially equally important evolutionary process as natural selection itself. The same is often said of the Baldwin effect. It constitutes a corollary process of selection (viz., organic selection) and is often considered to be an evolutionary mechanism or process (Bateson 2017a, 2017b).

According to the adherents of an extended evolutionary synthesis, we need to pay more attention to niche construction, organic selection and other neglected processes in which organisms play an active role in evolution. Allowing more processes to be considered *evolutionary* processes is one way we can do this (Scott-

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[10] A more general rendition of this view, in which not only behavioral but also morphological and physiological acquired characters are what initiates evolutionary change, is referred to as "plasticity-first" evolution (e.g., Levis and Pfennig 2016).

Phillips et al. 2014; Laland 2015). However, this solution has been met with some skepticism (e.g., Welch 2017; Scott-Phillips et al. 2014), as it is unclear whether granting something the status of an evolutionary process actually increases our understanding of evolution. Another problem with viewing niche construction as an evolutionary process that counteracts natural selection is that it still treats natural selection as an externalist environmental process. If niche construction "counteracts" the action of selection, selection must be a process that runs from the environment to the organism.[11] Instead, we should start from an ecological metaphysics of evolution (Walsh 2015).

3.5 An Ecological Metaphysics of Evolution

When Walsh (2015) calls for an ecological metaphysics of evolution, he highlights that we might have missed a lot in our understanding of evolution by not seeing organisms as active (and purposive) agents in their environments. Treating organisms as biological agents prior to being evolutionary agents is a necessary step in the direction of an ecological metaphysics (Walsh 2015). Biological entities are entities that interact with their environment. The relationship between the organism and the environment is crucial and in a sense prior to both the organism and environment themselves. As I argue in chapter 2, organisms and environments are *codependent* and *codetermined*. Without any organisms there would be no environments, and conversely, without environments there would be no organisms (Lewontin 1978; 2000). From an ecological metaphysics of evolution, then, the fundamental unit is that of organism-environment interactions. Evolution concerns changes in the types of interactions there are in a population. For the most part these interactions change in virtue of changes to organisms themselves, for example by organisms evolving faculties with which they interact with their environment in novel ways. Such kinds of changes to organism-environment interaction are captured by the theoretical framework offered by the modern synthesis. However, an environment can also change in such a way that organism-environment interactions change as a result, and more importantly, an organism can change the environment or its relationship to it such that the organism-environment interactions change (i.e., niche construction).

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[11] I will return to this point in greater detail in chapter 4.

Natural selection, then, is the process whereby organism-environment interactions are preferentially selected. It is concerned with the outcomes of organism-environment interactions over the life history of an organism (or at least to the end of its reproductive age) relative other members of its population. The strength of and response to selection is determined by the probability that advantageous interactions reoccur in subsequent generations, as well as their relative fitness impact. Consequently, advantageous hereditary traits (traits that are passed on through genetic inheritance) are more likely to spread than acquired traits whose likelihood of reoccurrence is lower. But it is in principle possible for selection to act on advantageous organism-environment interactions that are constructed or acquired (e.g., as a result of niche construction or behavioral plasticity).

Take gastrolith usage. Gastroliths are small stones that are ingested and then reside in the gastrointestinal tract of some animals. Carrying gastroliths is certainly an example of an acquired trait, as it is something the animal has to *acquire* from its environment to utilize. Usage of gastroliths is quite common among some groups of vertebrates and may serve a wide variety of different functions in relation to different environments (Wings 2007). For example, some have argued that in aquatic environments gastroliths might be used as ballast or for buoyancy control (Rondeau et al. 2005). While in terrestrial environments some have argued that gastroliths may supply minerals and help with trituration and mixing of foodstuffs (Wings 2007).

If, for instance, an organism enjoys a higher fitness relative to other members of its population as a result of having ingested gastroliths, natural selection will favor that individual. Further, let's say that this organism learnt to ingest gastroliths by observing its parents and continue the habit of ingesting such stones. If in the subsequent generations gastrolith ingestion is reliably transmitted through observational learning, and the fitness advantage is sufficiently high, natural selection could spread this trait throughout the population. Natural selection could also favor those who have a disposition for ingesting gastroliths, with or without observational learning, making it an acquired trait with a hereditary basis (which is an example of the Baldwin effect). For natural selection, however, the basis of which the gastrolith is ingested—be it by way of learning or instinct—is irrelevant as long as the stone is ingested. It is the outcome of the interaction—e.g., the improved trituration of foodstuffs—which is conducive to the fitness advantage, not whether or not it is learnt or instinctual, as long as the stone is reliably ingested.[12] More generally, we could say that the primary way in which genes matter for selection is in how conducive they are to the reliability and likelihood of advantageous organism-environment interactions to reoccur in subsequent generations. Taking this perspective on how natural selection acts, let us return to how we should interpret niche construction and the Baldwin effect. Are they different selective processes, as it is commonly argued?

3.6 Niche Construction and the Baldwin Effect Revisited

Both niche construction and the Baldwin effect have been seen as distinct evolutionary mechanisms or processes (e.g., Odling-Smee et al. 2003; Bateson 2017a, 2017b). Some even go as far as saying that they are different *selective* processes, as when niche construction is interpreted as a process where organisms counteract natural selection by modifying selection pressures (Laland 2015). The Baldwin effect is seen as a distinct selective process which operates on acquired traits until there is genetic variation present so natural selection can "take over" and consequently turn them into congenital traits.

I think these interpretations are misguided, and stem from viewing natural selection as a process of environmental filtration concerned with primarily with genes, i.e., from a "molecular" metaphysics of evolution. If we instead take the point of view introduced above, in which natural selection is concerned with the outcomes of organism-environment interactions and their reoccurrence, niche construction and the Baldwin effect are ways in which adaptation can occur and consequently be selected for. Niche construction is one way in which an organism can achieve a fitness advantage relative to other members of its population, but it is not a process that is counteracting the effects of natural selection. As long as the niche constructing behavior reoccurs reliably and the altered ecological conditions are reliably transmitted across generations it is no different from any other phenotypic trait in relation to natural selection. Acquired traits, and the Baldwin effect more generally, are also not selected initially by a process distinct from natural selection (i.e., organic selection). They are

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[12] Of course, if *all* members of a population ingest gastroliths, and some do it instinctually while others need to learn it through observation, natural selection will most likely favor the instinctual response because the trait itself (i.e., gastrolith ingestion) is presumably transmitted with a higher fidelity if it is congenital rather than learned.

selected for by natural selection from their first occurrence, it is just a shift in the system of inheritance that is responsible for the reoccurrence of the trait. Sometimes, it makes sense to say that an acquired trait has become a congenital trait, as for instance when a learnt behavior has become instinctual. However, in the case discussed above, the ingestion of gastroliths, it is unclear if it can ever fully be a congenital trait, as the key feature of having that trait is to *acquire* a suitable rock from the environment (though the disposition can certainly be congenital).

Natural selection understood as a process acting on the outcome of reoccurring organism-environment interactions has the benefit of being compatible with the main insights of the modern synthesis, while also allowing for the activities and behaviors of organisms to be included as ways in which organism-environment interactions can change and be acted on by selection, such as niche construction and the Baldwin effect. It also explains why the genetic system of inheritance is so central. First, it is the system of inheritance which is necessary for the development of most (if not all) phenotypes and consequently for there to be any organism-environment interactions at all. Second, it is the system of inheritance which enjoys the highest fidelity and stability in transmitting informational and causal resources necessary for the reoccurrence of favorable organism-environment interactions in subsequent generations. Finally, the ecological approach to natural selection can also explain how certain behavioral innovations, cultural traits, etc. can be selected for by natural selection, without being (directly) dependent on genetic variation or inheritance.

3.7 Conclusion

In this chapter I have argued that natural selection is standardly understood as a process of environmental filtration concerned primarily with genetic variation. Further, I followed Walsh (2015) in arguing that this stems from a gene-centered and externalist ("molecular") metaphysics of evolution. If we instead opt for an ecological metaphysics of evolution our understanding of natural selection becomes different. On such a metaphysics, natural selection becomes a process that acts on the outcomes of the advantageous interactions an organism has with its environment during its life history. As long as such interactions reoccur reliably in subsequent generations, natural selection will be insensitive as to what brings about these interactions, be it through genetic inheritance, social learning, cultural transmission, etc. A benefit of this view is that the ecological account of natural selection is compatible with the main insights from the modern synthesis, while also allowing for phenomena traditionally excluded from the modern synthesis, but emphasized by the extended evolutionary synthesis. Finally, the ecological view of natural selection can integrate some of these novel phenomena easily, without having to supplement and extend evolutionary theory with a host of new evolutionary processes. In the next chapter, I will show how the view introduced here influence the way we understand niche construction in relation to natural selection by comparing niche construction with sexual selection.

4

NICHE CONSTRUCTION, SEXUAL SELECTION, AND NATURAL SELECTION

4.1 Introduction

This chapter continues and develops the argument from chapter 3 with a special emphasis on niche construction. According to niche construction theory (NCT), niche construction is a neglected evolutionary process. On their view, niche construction is an evolutionary process in which organisms can change or create the environmental conditions from which natural selection acts (Odling-Smee et al. 2003). This conception has led the proponents of NCT to contrast niche construction with another evolutionary process, namely natural selection. They view niche construction as a process in which the causal arrow runs from organism to environment, whereas natural selection is a process in which the causal arrow runs in the opposite direction, from the environment to the organism (e.g., Laland et al. 2000; Odling-Smee et al. 2003). Niche construction then, is seen as a distinct selective process, albeit a very different one from natural selection (Laland 2015, 100). In other words, on traditional accounts of evolution by natural selection the causal arrow points from the environment to the organism. Niche construction theory adds a second process in which the causal arrow points from the organism to the environment in order to enable organisms to actively participate in evolutionary dynamics. This, the proponents of NCT argue, leads to a need for interactionist evolutionary explanations in cases where asymmetrically externalist explanations omit the active role of the organism.

Those skeptical of regarding niche construction as an evolutionary process, on the other hand, hold that there are only four evolutionary processes: natural selection, drift, mutation, and recombination. According to them, niche construction is, at best, a process which may indirectly alter the direction or rate of evolution, but should not be included among the fundamental evolutionary processes. Furthermore, they maintain that evolutionary processes directly alter the gene frequencies of populations. Niche construction is not such a process, because its influence on gene frequencies is only indirect through biasing the action of natural selection (Scott-Phillips et al. 2014).

Considering these disagreements, and the controversies about the extended evolutionary synthesis more generally (e.g., Laland et al. 2014a; Wray et al. 2014), this chapter will address the consequences of NCT's conceptualization of niche construction as an evolutionary process antiparallel to natural selection. As in chapter 3, I argue that understanding niche construction as an evolutionary process that runs in the opposite causal direction from natural selection inadvertently turns natural selection into a purely environmental cause of evolutionary change, which it is not. I further argue that a better way of conceptualizing niche construction in evolutionary theory is as a way in which organisms may alter their (expected) fitness during development. More generally, I argue that natural selection is concerned with *outcomes* (Lehrman 1970), and is agnostic with respect to the generative mechanisms producing the phenotypic variation (e.g., Griffiths and Gray 2001) or what mechanisms or entities creates or changes the environmental conditions to which an organism is exposed (Lewens 2019). I will show that, while important for evolution, niche construction should not be considered an evolutionary process that runs antiparallel to natural selection.

The main argument of this chapter is predicated on the idea explored in the preceding chapters, namely that the way we understand natural selection has a great influence on how we can conceptualize niche construction and its place in evolutionary theory. As in chapter 3, I shall defend an ecological view of selection. I end by arguing that such a view of selection is a perfectly reasonable way to interpret how natural selection is described by "standard" evolutionary theory.[13] Further, an ecological approach to selection also allows for the incorporation of causal factors other than environmentally produced selection pressures and genetic inheritance to have an influence in shaping evolutionary trajectories. That is, the ecological approach to natural selection allows for *interactionist* evolutionary explanations.

As we shall see, this has important consequences for the niche construction debate, but might also be a useful view for other debates which are ongoing under the umbrella term "the extended evolutionary synthesis" (Futuyma 2017; Laland et al. 2014a; Laland et al. 2015; Müller 2017; Pigliucci and Müller 2010; Wray et al. 2014; Welch 2017).

4.2 Externalist and Internalist Explanations in Biology

An important motivating reason behind the discussion of whether niche construction is an evolutionary process, and discussions about what causal factors in evolution are fully-fledged *evolutionary processes*, arose from niche construction theory's reaction to the "standard" explanatory structure of selection-based explanations (Odling-Smee et al. 2003, 371-78). Before we go into the standard explanatory structure of selection-based explanations, let us briefly examine the different kinds of explanatory structures we find in biology, as it will serve as a backdrop for the following discussion.

A common distinction that has been made is between internalist and externalist explanations (Godfrey-Smith 1996; Lewontin 2001). In relation to organic systems, an internalist explanation explains some properties of the system in terms of other properties internal or intrinsic to the system itself. An externalist explanation, on the other hand, explains some properties of an organic system in terms of the properties of their environments (Godfrey-Smith 1996, 30). Lewontin (1983, 2001) argues that the metaphors of development and adaptation carry internalist and externalist implications, respectively. Development, on the one hand, "carries the implication of an unfolding or unrolling of an *internal* program that determines the organism's life history from its origin as a fertilized zygote to its death" (Lewontin 2001, 55, my emphasis). Adaptation, on the other hand, carries an externalist implication: "[Adaptation] asserts

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[13] By 'standard evolutionary theory' I mean as it is presented in standard introductory textbooks, e.g., Futuyma and Kirkpatrick (2017) or Losos (2014).

that evolution consists in the shaping of species to fit the requirements of an autonomous *external* environment" (ibid., my emphasis).

One of the challenges for explanations in biology have been that organic systems are necessarily embedded in an environment, but each system—the organic and the environmental system—have traditionally been treated as separate causal systems. "That is, both in developmental and in evolutionary biology, the inside and the outside of organisms are regarded as separate spheres of causation with no mutual dependence" (Lewontin 2001, 55).

4.3 Selection-Based Explanations in Evolutionary Biology

In evolutionary biology, the most common explanation of the phylogenetic properties of an organic system is a *selection-based explanation* (Brown 2013). That is, when providing an "ultimate" explanation of the relevant organismic properties (it can be anything from adaptation, complexity, species diversity, etc.), it is primarily by reference to the action of natural selection on the ancestral organisms in the lineage leading up to the organism whose properties are being explained. More precisely, "they [selection-based explanations] refer to differences in the selection pressures acting upon populations at a given time that increase the probability of particular evolutionary outcome at some subsequent time" (Brown 2013, 555). As I briefly discussed in chapter 3, evolution by natural selection occurs in a population when three conditions (or principles) obtain (Lewontin 1970, 1978; Godfrey-Smith 2007, 2009): (1) there must be phenotypic variation amongst the individuals of a population, (2) the variation is (at least partially) heritable, and (3) the different variants produce a different number of offspring in the immediate or more remote generations.[14]

In an externalist selection-based explanation, the principle of variation and inheritance is assumed to be genetic. It is the principle of differential fitness which is used to predict and explain the distribution of the different variants of the population over generations. The fitness of a variant is measured by the (expected) reproductive output, and it can be inferred or hypothesized through looking at the "fit" of the individuals to their environment. That is, the principle of differential fitness assumes that there is phenotypic variation in the population, and that there are selection

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[14] There are several different ways of formulating these conditions and disagreement whether they are jointly necessary and sufficient. See Godfrey-Smith (2007, 2009) for discussion.

pressures acting on the population, specifically in regard to the focal trait or trait-cluster which is varying in the population. It is the outcome of the variants in dealing with selection pressures during their (reproductive) life cycle which is ultimately responsible for the realized fitness values of the individuals in a population. An explanation of the origins and maintenance of both selection pressures and variation is usually not necessary to form a selection-based explanation, but can be assumed, at least according to externalist explanatory framework.[15]

When explaining how the three conditions obtain, the standard practice has been to treat the organism and the environment as separate causal systems (Lewontin 2001). A selection pressure is commonly conceptualized as being constituted by the environmental system in relation to the organism. Abiotic factors such as temperature, humidity, altitude, etc. and biotic factors such as competition, prey abundance, pathogens, etc. put certain demands on an organism. These demands are features of the environment which impose themselves on the organic system in relation to how well the organic system performs. In this way, explaining the origins, changes, or maintenance of selection pressures amounts to explaining the origins, changes, or maintenance of environmental properties. And such properties are accounted for in terms of other properties of the environmental system—sometimes locally, other times globally, or by a mix of both.

The origin of heritable phenotypic variation is explained by reference to (primarily—at least on the "standard account") two processes: genetic mutation or recombination (for sexually reproducing organisms).[16] That is, variation among the

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[15] This is not to say that selection-based explanations are completely disconnected from questions regarding the origin and maintenance of selection pressures and of variation. In order to get a complete picture and explanation of evolution by natural selection, the principle of inheritance, the principle of variation, and the changes to and origins of selection pressures need to be explained. But for a selection-based explanation the details of inheritance, of variation, and selection pressures can be assumed to behave similarly as to what is already well established in the literature which deals with this in detail. Niche construction theory, as we shall see, do not think that selection-based explanation can always justifiably make such assumptions, specifically regarding the notion of inheritance and the dynamics of selection pressures.

[16] Though research in evolutionary developmental biology, or 'evo-devo', points to many other potential sources of phenotypic variation; changes to gene-regulation, robustness, modularity, and plasticity being the major new contributors (Brigandt 2015). For example, new phenotypic variation can originate through epigenetic processes where morphological and evolutionary novelty are the product of

individuals making up a population is explained in terms of properties internal to the population and internal to the individual organic systems themselves.

Finally, inheritance usually refers to the transmission of genetic material from parent to offspring through the genetic inheritance system or the genetic "channel of inheritance". The notion of "inheritance system" is an umbrella term used to describe the different mechanisms, processes, and factors that are responsible for the transmission and storage of hereditary information (Lamm 2018). What is of interest to us here, is that the genetic inheritance system is concerned with the transmission of DNA, the molecule which encodes genetic information and thus contains all the genes (and potentially far more) that play a role in creating the adult phenotype of the subsequent generation, from parent to offspring (Pearson 2006).[17]

We thus have internalist explanations for the principle of variation and inheritance, and for the origins and changes to selection pressures, which together are the preconditions for there to be heritable differential fitness. The principle of differential fitness is based on the relationship between the properties of the varying phenotypes in a population and selection pressures acting on that population, and the resulting distribution of phenotypic variation over generations is explained from principles of population dynamics. Chester (2012), for example, argues that there is an overriding principle of nature which governs any population's behavior: "The effect on the environment of a population's success is to alter that environment in a way that opposes the success" (Chester 2012, 289). That is, the principle of differential fitness itself can be explained in terms of population-dynamical principles (i.e., Malthusian growth) coupled with assumptions about the nature of organisms and the environment, and the nature of the interaction between them (i.e., the principle of variation and inheritance, and the origins and changes to selection pressures). This principle is at the

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phenotypic plasticity or through induction by environmental cues (e.g., Gilbert and Epel 2015; West-Eberhard 2003, 2005; Müller 2003; Sultan 2015).

[17] There is an ongoing controversy concerning the relative importance of different inheritance systems in evolutionary biology. Lamm (2018) points out three different camps: Monism: the gene-centric position. Holism: developmental systems theory (Oyama 2000; Oyama et al. 2003). Multiple systems of inheritance: e.g., ecological inheritance (Odling-Smee et al. 2003), epigenetic, behavioral and symbolic inheritance (Jablonka and Lamb 2014), cultural inheritance (e.g. Boyd and Richerson 1985; Cavalli-Sfroza 1981; Durham 1991). As I argued in chapter 1, I think the importance of different systems of inheritance is an empirical and context-sensitive question.

heart of selection-based explanations, and connects the variation among individuals in a population with selection pressures acting on the population in order to help explain the resulting dynamics of the distribution of the heritable phenotypic variation of a population over generations.

The selection-based explanation explains how the phenotypic variation has been distributed over generations leading up to the focal trait or trait-cluster in the population. It explains why different variants have been differentially selected. The standard structure here is *asymmetrical externalism* (Godfrey-Smith 1996; Odling-Smee et al. 2003). The differential selection of variants is explained in terms of how the variants cope with the demands issued by the environmental system (figure 4.1). Changes in the distribution of properties of the individuals of a population are explained in terms of *external* environmental properties. However, the selection pressures themselves are explained in terms of properties *internal* to environmental system.

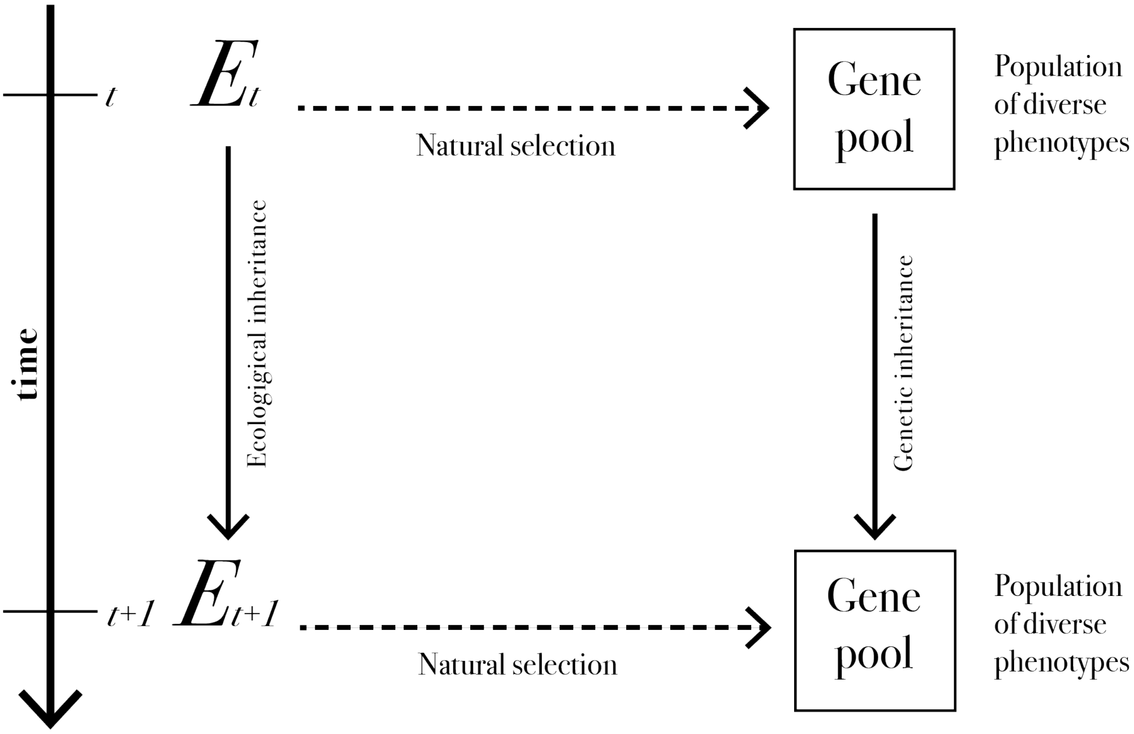

Figure 4.1. Asymmetrically externalist explanations. The environment is the agent of selection, and causally explain the distribution of different phenotypes in a population over time. The phenotypes that best fit E (at both time t and time t+1) are selected. While the properties of E (at both time t and time t+1) are causally decoupled from the activities of the population of organisms. (adapted from Odling-Smee et al. 2003, 14)

To illustrate the asymmetrically externalist explanatory structure, consider a favorite example of natural selection in action from evolutionary biology: the explanation of the rapid changes in the distribution of melanic morphs in the peppered moth (*Biston betularia*) in Britain during the 19th and 20th century (e.g., Tutt 1891; Haldane 1924; Kettlewell 1955; Majerus 1998). The typical morph of the peppered moth is pale gray, while some variants have a single genetic mutation that causes melanism (a dark coated morph). Melanistic morphs are generally easily spotted by birds, which prey on them when they rest on trees. By contrast, the gray morph is camouflaged, as its coloration is similar to the bark and lichen of the trees. However, during the 1800s, there was a significant increase in the number of melanic morphs in the peppered moth populations in Britain. How can we explain this increase? The increase and spread of melanic morphs (and the subsequent decline of the morph in the 1960s) is explained by the dramatic changes in the environment of the peppered moth. During the 1800s and well into the 1900s, the massive amount of coal burning increased air pollution and consequently the trees the peppered moth rested on were coated by soot. This made the surface of trees darker and consequently made the typical gray morph more prominent to birds that prey on them. The melanistic morphs, however, were concealed by the darkened surface and thus more often eluded the birds, gaining an increase in fitness, nearly driving them to fixation in the late 1800s (Tutt 1891). After the 1960s, the burning of coal was significantly reduced and the fitness advantage the melanic morphs declined as the trees became lighter.

When explaining the distribution of the novel phenotype in the population over generations, the environmental properties are conceived as selection pressures and consequently explain why the melanistic morph enjoys higher or lower fitness depending on the amount of soot on the trees. In other words, the environmental properties explain the distribution of the organismic properties over time, whereas the environmental properties themselves are neither influenced by nor explained by the activities of the peppered moths, but rather by factors internal to the environmental system itself. This is what makes a selection-based explanation *asymmetrically externalist*. To sum up, organisms vary within populations, those variants that perform best in their given environment are selected, and the environment itself is ruled by its own intrinsic dynamics. Natural selection is conceived as an external agent, acting from the environment to the organism (as in figure 4.1).

While this is unquestionably an elegant explanatory structure, it carries some assumptions that have recently been challenged. One such assumption is that an organism's niche is a preexisting environmental configuration that that the organism passively gets fitted into through the action of natural selection. Niche construction theory uses theoretical and empirical examples to challenge this (amongst other) assumption.

4.4 Niche Construction and the Challenge to Asymmetrical Externalism

The causal direction of natural selection on the asymmetrically externalist picture is unidirectional—from environment to organism. However, all organisms interact with their environment and change it (to a greater or lesser degree) as they do so (Odling-Smee et al. 2003). No one disagrees with this. There is disagreement, however, on the significance of these interactions for evolutionary theory. Niche construction theory captures the cases where organisms actively modify their environment, or their relationship to it, in a way that alters their selective environment (Laland et al. 2016). This constitutes a general case which is incompatible with an asymmetrically externalist explanatory structure.

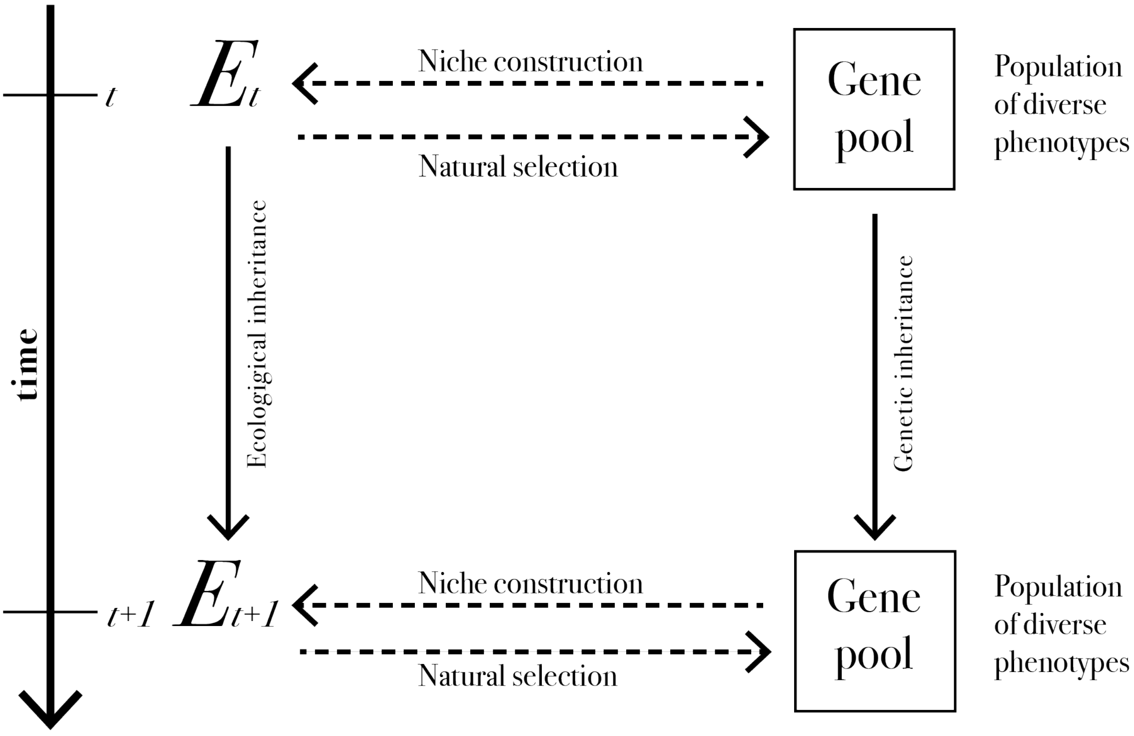

Figure 4.2. Interactionist explanations. In addition to natural selection, organisms actively change the environmental conditions, E, through niche construction. Here the two causal

domains—the organisms and the environment—act on each other. Niche construction is an additional process, going the opposite direction of natural selection, thus modulating the selection pressures acting on the population of phenotypes over time. (adapted from Odling-Smee et al. 2003, 14)

As we can see in figure 4.2, niche construction includes the active modification of environment by the organisms in selection-based explanations of adaptive evolution. Additionally, organisms inherit the modified environmental conditions for the previous generation, further affecting how natural selection acts on the population. In cases where organisms are engaged in niche construction, there is a reciprocal causal relationship between organism and environment. The effects of the niche construction activities on the environment modifies the selection pressures acting on the individuals in a population, as well as future selection pressures if the modified ecological conditions are inherited. The stronger the feedback between organism and environment, the less appropriate an asymmetrically externalist explanation will be. The cases with strong feedback can only be explained by an *interactionist explanation*, in which the active role of the organism in shaping its environmental conditions is included.

If we take this view seriously, several questions arise. How should we interpret the reciprocal causal relationship between organisms and environment, and what are the consequences of such an interpretation for evolutionary theory more generally? That is, what kind of process is niche construction? And how does it relate to other evolutionary process, specifically natural selection?

4.5 Why Niche Construction is Not an Antiparallel Process to Natural Selection

As we saw above, the niche construction perspective grew out of a dissatisfaction with the asymmetrically externalist reification of the causal structure of selection-based explanations (Lewontin 1983b, 2001; Levins and Lewontin 1985; Godfrey-Smith 1996; Odling-Smee et al. 2003). A consequence that follows from the assumptions of the externalist approach is that organismic activity, or the agency of organisms is completely left out, and thus potentially leaving an "explanatory gap" for cases in which organisms are engaged in activity or behavior which influence their fitness (Laland et al. 2019). NCT proposes that niche construction capture and account for such cases. Niche construction is then conceived as a second process, in addition to, and antiparallel to, natural selection, whereby the activities and behaviors of organisms bias the action of selection:

> The directionality of niche construction results from the expression of genetic and acquired (e.g., learned, brain-based) semantic information: information specifying how organisms should operate in their local environments in order to satisfy their requirements. This information would be eradicated, by selection, or through learning, if its average effect on fitness was negative. It follows that niche construction is a selective process (albeit very different in form to natural selection), since it requires an ability on the part of organisms to discriminate, and actively sort between environmental resources, and hence to change the physical state of some factors in their environments in beneficial ways. (Laland 2015, 100)

These two processes are connected through a reciprocal relation between organismic activities (niche construction) and environmental conditions (selection pressures) over the life cycle, and potentially over several generations through the transmission of altered environmental conditions through ecological inheritance, as well as genetic inheritance (figure 4.2). As Laland et al. (2013) put it:

> [A] major consequence of this externalist assumption is that it hinders the environment-altering activities of organisms from being treated as evolutionarily causal (Odling-Smee et al. 2003). Darwin's natural selection is fully compatible with the externalist assumption because the 'causal arrow' of natural selection points in the 'right' direction, from environments, to organisms, and so it is natural to describe natural selection as causing adaptations. However, the causal arrow of niche construction points in the 'wrong' direction, from organisms to their environments. (Laland et al. 2013a, 730-731)

However, when we examine the interpretation of the causal structure of interactionist explanation offered by NCT (as in figure 4.2), natural selection is conceived of as an *external process* acting from the environment to the organism (e.g., Odling-Smee et al. 2003; Laland 2015). Adding niche construction as a different process running the opposite causal direction of natural selection (i.e., from organism to environment) effectively equates natural selection with an environmental process acting on organisms.

Natural selection is not solely an environmental process. It is not sensitive to whether the reproductive success of organism is created either by environmental conditions acting on organisms, organisms changing the environment to better suit their properties, or a mixture of both (Lewens 2019). Rather what natural selection is sensitive to is the *outcome* of organism-environment *interactions* over a reproductive life cycle and the extent to which such interactions *reoccur* in subsequent generations (Lehrman 1970; Griffiths and Gray 2003; see also chapter 3). These two things; the outcomes of organism-environment interactions and their reoccurrence over generations, is the causal engine of natural selection—not the environmental conditions alone. The environmental conditions are an important factor, they are an essential part of the organism-environment interaction. And in many cases just referencing the changes to the environment is enough to explain the distribution of a phenotypic trait in a population. A perfectly good example of this is the peppered moth case discussed earlier. In that case, the changes to the environmental properties changed the outcome of the organism-environment interactions of the individuals composing the peppered moth populations in Britain, such that natural selection favored the melanistic morph. But the soot on the trees alone is not natural selection. It is the matching between the soot on the trees and the melanic form, and the consequences this match had for the organism-environment interactions over the reproductive life cycle of the peppered moths. Thus, in this example, environmental conditions are the important "causal difference makers" in explaining the sudden increase and decrease in the distribution of melanistic forms in the peppered moth populations in Britain. But this does not mean that all selection-based explanations share the same causal structure, as niche construction theory have pointed out (Odling-Smee et al. 2003; Laland et al. 2013a). In fact, externalist explanations might rather be the exception. Consider this imagined example. In industrial Britain, grey colored morphs of the peppered moths were easy prey for birds, because they were conspicuous when resting on soot-covered trees. Let's now imagine that some individuals started to rest on white and grey cladded houses. These grey morphs did not suffer the same high predation risk of their tree-resting counterparts and consequently had more offspring.

In this case, the activity of the organism—the changed preference of resting surface—counteracted the high predation risk associated with resting on trees covered by soot. On niche construction theory this would be a perfect example of counteractive relocational niche construction—where organisms actively modify their selective environment as a response to changes in environmental conditions in virtue of changing their spatio-temporal "address" (Odling-Smee et al. 2003; see also chapter 6). This would then constitute a case in which some peppered moths changed their selective environment by relocating to a novel selective environment. On the causal picture presented in figure 4.2, this instance of counteractive relocational niche construction is conceived as a distinct process running the opposite direction of natural selection. That is, as a process counteracting (or biasing) the action of selection.

On the externalist view, this example would primarily be explained in terms of environmental conditions—those grey morph peppered moths that happened to rest on white and grey cladded houses were not exposed to the same selection pressures as their tree-resting counterparts. Consequently, the individuals with a preference for resting on houses had more offspring and were favored by natural selection.

I think both explanations are misguided. On the externalist picture, a potentially important part of evolutionary dynamics—what individual organisms *do* during their life cycles—is "black-boxed". The activities of organisms may be a critical factor in selection-based explanations, and organism-environment interactions are constituted of both *organisms* and *environments*. Neglecting the activities of organisms can lead to an omission of salient explanatory information (Laland et al. 2019). The niche construction perspective rightly includes the active role of the organism, but in doing so renders natural selection as an environmental process acting on organism.

A more appropriate explanation lies somewhere in between—the grey morph peppered moths that "chose" white and grey cladded houses as a resting surface changed the space of possible interactions with their environment, resulting in a different outcome of organism-environment interactions over their life cycle. Natural selection, acting on the outcome of such interactions, differentially selected those that exhibited a preference for the white and grey cladded resting surface. In this case, natural selection is not a process acting on the organism from the environment, and organisms can be active participants in their own evolution.

Another example that illustrates the problem of conceiving niche construction as a distinct evolutionary process that runs in the opposite causal direction of natural selection, and the inadequacy of purely externalist explanations, can be seen by looking at different ways sexual selection occurs in birds.

4.6 Sexual Selection and Niche Construction in Peafowls and Bowerbirds

Birds exhibit some of nature's most powerful examples of sexual selection. Sexual selection in the peafowl has resulted in a sexual dimorphism in which the male bird, the peacock, sports a magnificent (and possibly maladaptive) train of elongated and colorful tail coverts. The peahen, on the other hand, has a much smaller train and less colorful plumage overall.

Another family of birds, the bowerbirds (e.g., the satin bowerbird, *Ptilonorhynchus violaceus*) show less of a spectacular morphological sexual dimorphism, but an impressive difference between the behavior of the sexes. Male bowerbirds build complicated nests which female bower birds inspect before choosing a mate. These nests are complex physical structures which are decorated with ornaments with which a suitor tries to impress the female to mate.

The explanation of such sexually dimorphic traits in birds is most commonly done by reference to sexual selection, specifically by mate choice theory (Satin bowerbirds: Coleman et al. 2004; Peafowl: Loyau et al. 2008). In such explanations, it is common to attribute certain preferences to the female when choosing a mate, and the male which possess the traits that best matches those preferences will have more offspring. On an externalist explanation, the female preferences work in a similar fashion as the environmental condition (or selection pressure) in other selection-based explanations. As such, those males that conform to the female preferences are sexually selected. However, as Laland et al. have pointed out (Laland 2011; Laland et al. 2013a), such an explanation leaves out the explanation of the origin of the female preference and the coevolution of the female preference and the focal male trait of that preference. The mechanisms responsible for mate preferences is a controversial issue in theories of sexual selection (Andersson 1994; Kokko et al. 2003; Ryan 2018), however the details are not crucial for this discussion. An externalist explanation is insufficient because it does not account for the reciprocal relation between the peahen's preference and the male train (or a combined set of peacock features; see e.g., Takahashi et al. 2008; Loyau et al. 2008 for discussion) over generations. The same is true of the bowerbird, in which the nest-building behavior of the male and mate preference in the female bowerbird are reciprocally linked. A purely externalist explanation omits the fact that the female choice itself evolves as the male trait evolves, something which is included in an interactionist explanation (Laland et al. 2011). However, if niche construction is an additional and antiparallel process to natural selection (as the causal structure NCT seen figure 2 suggests), it is surely also a different process from sexual selection. How, then, should we interpret the apparent niche construction activities of the bowerbirds? A male bowerbird is altering its environment (building a bower) which consequently alters the (sexual) selection pressures acting on it. But is this a process that runs in the opposite direction of sexual selection? The activity of the male bowerbird is certainly crucial, but does an invocation of niche construction help explain this trait and the consequent coevolution of the female preference? Further, how do we explain the apparent similarities between the dynamics of bowerbird sexual selection and peafowl sexual selection if one of these trajectories are influenced to large extent of a second process running in the opposite causal direction (i.e., niche construction)?

If, as we did with natural selection above, we think of sexual selection as a process that is concerned with outcomes of interactions, things become a little clearer. The nest-building activity of the bowerbird is just one way of many that a match between mate preference and focal trait can be established between mates. The morphological sexual dimorphism of the peafowl is another. The selective process is sexual selection, a mate preference may be linked to the morphology or the behavior of the chosen mate, or both. Just as with natural selection, sexual selection is not sensitive to what caused the match just that there is a match and that such a match reoccurs is a similar fashion over generations.

One could, in principle, object to the aforementioned problems by holding that the sexual selection in both the peafowl and bowerbird are actually instances of niche construction. However, there are at least two problems with such a strategy. First, it is unclear what advantage we get from relabeling sexual selection as niche construction, seeing that explanations and mathematical models of 'runaway' sexually selected traits and the reciprocal dynamics of sexual selection in general have existed since Fisher (1915). Second, since the notion of niche construction is predicated on organisms' *active* modification of their or each other's selective environment, the difficulties of accounting for the difference between the behavioral trait of the male bowerbird and the morphological trait of the peacock in establishing a mate preference seem to remain—which could be accounted for by adopting a more nuanced interactionist view in which niche construction is one of several ways a mate preference can be established. On this view sexual selection are instances where *interactionist explanations* are needed, but a second *antiparallel process* acting in the opposite direction of sexual selection is not.[18]

4.7 Interactionist Explanations in Evolutionary Theory

Asymmetrically externalist explanations have been powerful in evolutionary theory and are in many cases appropriate for providing a selection-based explanation of certain traits or clusters of traits. However, niche construction theory has rightly pointed out that in many cases this explanatory structure is a simplification which omits potentially important explanatory detail (Laland et al. 2019). All organisms necessarily interact with, and change, their environment during their life cycle (Odling-Smee et al. 2003), and those interactions might carry significant explanatory weight. Moreover, new research in evo-devo, eco-devo, and eco-evo-devo[19] have highlighted the importance for development and evolution of biological interactions—organism-organism interactions (Gilbert 2014) and especially organism-environment interactions (Moczek 2015; Sultan 2015; Gilbert and Epel 2015). Emphasizing the importance of reciprocal causation between the organism and its environment in evolution, how organisms can inherit more than just the genetic material of the ancestors through ecological inheritance, and the resulting influence these features have on evolutionary dynamics is an important feat that niche construction theory has played a central role in recognizing (Laland et al. 2019). The overarching theoretical consequence is that selection-based explanations are not necessarily externalist, but may also be interactionist. While the relative frequency of instances in which interactionist explanations are necessary is an empirical matter (Schulz 2014), niche construction theory at least shows us that interactionist explanations are not something

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[18] One might object here and say that on the more "nuanced" interactionist view, sexual selection will not be a distinct process from natural selection. I am perfectly happy with sexual selection being a special instance of natural selection in which there is a co-evolution and co-dependence on selection pressure and traits in due to sexual dimorphism, which gives a strong reciprocal dynamic.

[19] See Carroll (2005) and Amundson (2005) for treatments of the science of evo-devo and Sultan (2015), Abouheif et al. (2014), and Gilbert and Epel (2015) for treatments of eco-devo and eco-evo-deo.

which can be ruled out a priori (Odling-Smee et al. 2003). We must always make simplifying assumptions, but the generality of such simplifying assumptions is increasingly being called into question (Moczek 2015).

However, as we have seen above, interpreting niche construction as an additional and antiparallel process to natural selection vindicates an externalist interpretation of natural selection as a process driven solely by environmental conditions acting on otherwise passive organisms. This interpretation of natural selection is what niche construction theory originally objected to (Lewontin 1983a; Odling-Smee et al. 2003; Laland et al. 2019). This problem arises for niche construction theory because niche construction is interpreted as an antiparallel process to natural selection. However, the inclusion of interactionist explanations in evolutionary biology does not require that we add niche construction as an additional process that bias the dynamics of the "original" evolutionary processes (viz., natural selection). Interactionist explanations are perfectly compatible with natural selection being the primary causal factor in in explaining the distribution of phenotypic variation, and consequently the primary driver of adaptive biological evolution. What we need to establish is how interactionist explanations influence the assumptions we have on *how* natural selection brings about evolutionary change.

4.7.1 Two Interpretations of Interactionist Explanations

As we saw above and in chapter 3, the asymmetrically externalist view takes the causal engine of natural selection to be the environment. The environmental conditions are responsible for the changes in the distribution of phenotypic variation in populations, but the environmental conditions themselves are explained in terms of local and global changes in the environmental systems itself (e.g., volcanic eruptions, droughts, seasonal fluctuations in temperature, etc.). It is important to recognize that externalism is an *explanatory strategy*, and it is not necessarily the case that these explanations fully track the causal structure of evolutionary trajectories and even evolutionary theory. It is an assumption made based on what causal factors should be included in an explanation and which can be rendered as background conditions. Niche construction theory has made a convincing argument that the externalist assumption is not generalizable and that many causal factors that have previously been treated as background conditions should be explicitly included in explanations. If one finds this argument persuasive, as I do, we need to look at our assumptions concerning the fundamental principles of evolutionary theory and see how they are affected by an inclusion of interactionist explanations. I think there are two strategies here. First, we can follow NCT in adding another process with an opposite causal direction of natural selection—i.e., a process that runs from the organism to the environment. This view allows for a reciprocal relationship between environment and organism, and the active role of organisms in evolution, but still renders natural selection *an external and environmental process*, albeit a modifiable one.

A second strategy, which I introduced in chapter 3 and above, is to revisit our assumptions concerning natural selection in the first place. On this view we can see niche construction as an example that shows us that natural selection is *not* an externalist process driven by environmental conditions acting on passive populations.[20] I have already given reasons above for why I think the first strategy is misguided. Now I will attempt to give some reasons for why I think the second strategy is more promising.

4.8 The Selection on Outcomes of Favorable Interactions

Let us start out with a general description of natural selection:

> Natural selection occurs whenever there is a consistent, average difference in fitness (reproductive success) among sets of "individuals" that differ in some respect that we may refer to as phenotype. (Futuyma 2014, 189).

Most biologist would add that the difference amongst the phenotypes must be heritable, but not all (e.g., Brandon 2006, 2008). The first thing to notice is that the above definition carries no assumption on the causal directionality of natural selection. In fact, as some have argued, natural selection may be a population-level statistical summary of individual-level organism-environment interactions (Matthen and Ariew 2002; Walsh et al. 2002; Walsh 2007; Futuyma 2014; Futuyma and Kirkpatrick 2017). I will not rehearse the statisticalists vs. causalists argument here (see Ramsey 2013a,

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[20] 'Passive' here should be understood as regarding the effect individual organisms or populations of organisms can have on their selective environment. Passive organism are just recipients and not participants in their selective environments.

2013b for arguments in favor of a causalist position), but simply note that if the statisticalists turns out to be right, it constitutes a challenge to the first strategy for incorporating interactionist explanations in evolutionary theory, and not the second strategy. But even if we grant causal efficacy to natural selection, it is not clear that it turns out to be an externalist causal process acting from the environment to the organism. If we return to the characterization of natural selection above, the critical concepts are *consistency*, *fitness differences among individuals*, and *phenotype.* The *fitness difference* arises from the difference in phenotype in relation to environmental conditions relative to the other members of the population—it concerns the outcomes of individual organism-environment interactions in a given population. The *consistency* concerns the fact that the same phenotype consistently creates the same fitness impact (e.g., canine and carnassial teeth consistently help mammalian predators in successfully capturing and eating prey). If the fitness impact of a trait would be inconsistent, it would significantly weaken the directionality and rate of selection on the trait in question.

The notion of phenotype refers to "[t]he morphological, physiological, biochemical, behavioral, and other properties of an organism manifested throughout its life" (Futuyma and Kirkpatrick 2017, G-13). The *outcomes* of the interactions between phenotype and environmental conditions over the organism's life cycle—relative to other members of the population—is what realizes the differential reproductive success amongst the individuals of a population (Lehrman 1970; Griffiths and Gray 2001). Natural selection is insensitive to what developmental or environmental routes which can produce favorable interactions, only that they have a consistent fitness impact and reoccur in subsequent generations (i.e., that the fitness impacts are heritable in some manner). The reoccurrence does not *have* to occur through genetic inheritance. Natural selection is not sensitive to the what mechanisms created the interactions nor what mechanisms is responsible for their reoccurrence, only that they are have a consistent effect on fitness and that they reoccur. The developmental route responsible for fitness differences amongst members of a population might be a single point mutation that creates a novel morph, as with the peppered moths (Majerus 1998). Or it might be through an organism's modification of environmental conditions to better suit is morphology, as is the case with many instances of niche construction (Odling-Smee et al. 2003). This point has been made earlier and is a central aspect of developmental systems theory (Oyama 2000; Oyama et al. 2001; Griffiths and Gray 2001), and I think the point is worth revisiting. In a time in which there is significant polarization between different groups of evolutionary theorists under the discussion of an extended evolutionary synthesis (e.g., Laland et al. 2014a; Wray et al. 2014; Gupta et al. 2017a, 2017b; Feldman et al. 2017), it is important to highlight the parts of evolutionary theory that can still work together. Interactionist selection-based explanations are not in conflict with standard evolutionary theory, as long as we do not reify the principles of natural selection in an externalist and gene-centric manner. However, adding niche construction as an additional process going the opposite causal direction of natural selection further entrenches such an externalist reification, and consequently does a disservice to the central point that the niche construction perspective has spent so much energy trying to establish—namely that organisms are evolutionary agents which through their activities and behavior partially inform their developmental and evolutionary trajectories (Laland et al. 2019). This, however, should not lead to an undermining of the effects the active role of the organism and ecological inheritance can have on evolutionary dynamics—which is a potentially crucial component in providing adequate selection-based explanations of evolutionary systems (Bateson 2004, 2017a, 2017b; Walsh 2015).

4.9 Conclusion

In this chapter I have argued that conceiving niche construction as an additional process that run in the opposite causal direction of natural selection renders natural selection into an externalist process. I then developed the argument from chapter 3, that there is no reason to hold that the causal engine of natural selection are only environmental properties, and that a more precise interpretation of natural selection is as a process acting on the *outcomes of (reoccurring) organism-environment interaction over an organism's life cycle*. Instead of adding a process going in the opposite causal direction of natural selection to accommodate for the reciprocal influence between organism and environment in shaping the selective environment, we should interpret natural selection as an *ecological process*. This allows us to invoke interactionist selection-based explanations, highlighting how different developmental and ecological processes (e.g., plasticity, niche construction, sexual selection, etc.) can play an important explanatory role in selection-based explanation without having to stray far from how the principles of natural selection are understood to work in "standard" evolutionary theory. In the next chapter I will look at some other arguments made in connection to how we conceive of the relationship between developmental and behavioral processes and evolutionary processes in connection to the proximate-ultimate distinction introduced by Mayr (1961).

5

ORGANISM-ENVIRONMENT INTERACTIONS AND THE PROXIMATE-ULTIMATE DISTINCTION

5.1 Introduction

The debate around the causal structure of evolutionary theory has recently centered on the question of evolutionary causation (e.g., Uller and Laland 2019; Dickins 2020). This debate surfaces in many other ongoing controversies in evolutionary theory such as in the debates discussed in chapter 3 and 4—on reciprocal causation and asymmetrical externalism—as well as debates concerning reaction norms and constructive development, the modern and extended synthesis, and the proximate-ultimate distinction. The debate around the proximate-ultimate distinction is the topic of this chapter. Proponents of an inclusive view of evolutionary causation—a view in which individual-level and developmental processes can sometimes be seen as evolutionary causes—argue that the causal structure of evolutionary theory implied by the distinction between proximate and ultimate causes exclude developmental processes and causes from being considered evolutionary causes (Laland et al. 2009, 2011, 2013a, 2013b; Laland 2015; Uller and Laland 2019). As they put it:

> From this perspective [from the perspective of a distinction between proximate and ultimate causes] there is no room for proximate causes in evolutionary explanations since only genes are inherited, effectively preventing nongenetic developmental causes from becoming evolutionary causes. (Uller and Laland 2019, 3)

These authors consequently aim to undermine the proximate-ultimate distinction to make room for a larger set of causes evolutionary causes to figure in explanations of evolutionary outcomes. I shall look at two of the arguments which the proponents of an inclusive view of evolutionary causation offer in doing this: (1) the causal parity argument (or the argument from constructive development), and (2) the causal incompleteness argument (or the argument from reciprocal causation). The causal incompleteness argument concerns cases in which evolutionary outcomes are insufficiently explained if only ultimate (viz., evolutionary) causes are invoked. The causal parity argument concerns the causal structure of development and the consequences of what different views about this structure have for evolutionary causation.

I will argue that neither of these two arguments are convincing. At the heart of the matter lies an unjustified identification of proximate causes with developmental causes, and ultimate causes with evolutionary causes, which I shall refer to as the *identity assumption*. However, I will show that neither the causal parity argument nor the causal incompleteness argument holds even if we grant the identity assumption. Instead of identifying proximate and ultimate causes with evolutionary and developmental causes, we should rather interpret the proximate-ultimate distinction as being a distinction between triggering and structuring causes (Dretske 1988). On this view ultimate causes are those that can be interpreted as the structuring causes of evolutionary events, while proximate causes are those that trigger individual-level developmental processes and ecological interactions. All it takes for something to count as an ultimate cause is for it to be a structuring cause influencing the action or outcome of a population-level process that leads to an evolutionary response. This approach allows developmental processes, such as niche construction, plasticity, learning—as well as environmental processes, such as volcanic eruptions and glacial retractions—to count as ultimate causes and thus serve an explanatory role in evolutionary explanations.

The structure of the chapter is as follows. First, I introduce the proximate-ultimate distinction and what I take to be the important motivation behind its introduction by Mayr (1961). Then introduce the causal incompleteness argument and the causal parity argument and the rebuttals to these. After that I introduce the distinction between structuring and triggering causes and use that to offer interpretation of ultimate causes as structuring causes of evolutionary outcomes and proximate causes as triggering causes of development and individual-level ecological interactions. Finally, I show how such an interpretation of ultimate causation allows for individual-level developmental (and environmental) processes to be explanatorily and causally relevant in evolutionary theory in virtue of structuring the action of population-level processes, or otherwise being a structuring cause of population-level outcomes.

5.2 The Distinction Between Proximate and Ultimate Causation

In a foundational essay on concerning the concept of causation in biology Mayr (1961) proposed a distinction between proximate and ultimate causes. The distinction is offered to illustrate two distinct ways in which biologists invoke causation to ask and answer different questions (*Fragestellung*) about biological phenomena. Both proximate and ultimate questions invoke the concept of causation in unique manner which differs from how causation is used and understood in the other sciences—especially classical mechanics, which was a central point Mayr aimed to demonstrate. According to Mayr, the general concept of causality contains three epistemological elements. Explanation of past events in terms of their antecedent causes, prediction of future events, and as interpretation of (apparently) goal-directed—or teleological—phenomena (Mayr 1961, 1501). However, biological systems are inherently different from the physical systems of classical mechanics. In particular, biological systems exhibit goal-directedness and (radical) indeterminacy. These two features significantly alter the way in which biological causation can be invoked in explanation and prediction compared to classical mechanics. The indeterminacy of biological systems is responsible for the difficulty of predicting outcomes or events in biology. Biological systems are indeterminate due to their complexity (the integration and interaction of parts across multiple scales of spatial and temporal organization) and the randomness of the significance of events (e.g., a random point-mutation can produce a novel phenotype with significant fitness advantages, or a random ecological encounter could have drastic cascading effects). Accordingly, Mayr argues that biological causation will at best only be statistically predictable.

Biological systems also exhibit goal-directedness. The physical systems of classical mechanics, in contrast, are either non-teleological or teleological *by design* (e.g., human artefacts). When explaining the goal-directedness of designed artefacts, the goal of the artefact—or its *final* cause—can be employed as an antecedent cause which explains *why* the artefact was designed as it was (and not any other manner). However, using the goal as an antecedent cause in an explanation of the goal-directedness exhibited by biological systems is problematic. Since we do not wish to attribute an intention or a plan to the natural world in general, we need a way to account for the origins of the goal-directedness that we readily observe in biological systems without invoking any form of prior intention or design—i.e., without a *final* cause.

Evolutionary theory offers a solution to this problem through the process of natural selection. By linking the goal-directedness of traits and processes to their adaptive significance (or function) in a population of varying individuals, and assuming that the information needed to recreate the (goal-directed) traits and behaviors in succeeding generations are transmitted through (genetic) inheritance, natural selection is able to produce goal-directed traits and processes without the goal being an antecedent cause, but rather population-level outcome. In other words, natural selection can produce goal-directed systems without itself being a goal-directed (or purposive) process. Biology is thus unique in having systems whose features and behaviors can be explained in terms of their purpose (biological function/ adaptive significance), while the origins of such features simultaneously being an outcome of a purposeless process (i.e., natural selection). This uniqueness results in biology being separated into two different fields which differs in methodology (Mayr uses the German word *Fragestellung*—which can be translated into something like "way of posing/asking questions"). On the one hand you have biologists that ask *how* particular organisms develop and operate in their environment. On the other hand, you have biologists that ask *why* the organism operates in that way and not another. The causes that explain a question of the former are different from the causes that explain the latter. It is in this context Mayr offers the distinction between *proximate* and *ultimate* causes:

> [P]roximate causes govern the responses of the individual (and his organs) to immediate factors of the environment while ultimate causes are responsible for

> the evolution of the particular DNA code of information with which every individual of every species is endowed. (Mayr 1961, 1503)

To illustrate, consider Mayr's own example. "Why did the warbler at my summer place in New Hampshire start his southward migration on the night of the 25th of August?". This question has two very different, but mutually informative answers, both of which constitute an explanation of the phenomenon. First, we can answer the question by giving an account of the evolutionary history leading up to the warbler's migration behavior. This explanation would invoke what Mayr calls the ecological and genetic causes of the warbler's migration: "The warbler, being an insect eater, must migrate, because it would starve to death if it should try to winter in New Hampshire" (Mayr 1961, 1502). Natural selection will favor those that have a (genetic) constitution which predisposes them to migrate south at the right time given the appropriate environmental stimuli. This, in turn, explains *why* the individual warbler will migrate. These are what Mayr calls *ultimate causes* and are causes used in the explanation of the evolutionary history of a trait.[21]

We could also answer the question by providing an account of the physiological mechanisms responsible for the migration in the individual warbler. Such an explanation would refer to mechanisms responsible for photoperiodicity in the warbler (i.e., its sensitivity and response to the relative length of light and dark periods) coupled with relevant environmental conditions that play a role in initiating the migration (e.g., shorter days, colder nights). This, in turn, explains *how* the warbler manages to migrate at the correct time of year. These are examples of the *proximate causes* and are used in the explanation of the causal mechanisms of an individual warbler as it interacts with its environment.[22]

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[21] One quibble with Mayr's explanation: The New World warbler (*Parulidae*) is a family of tropical birds thought to have originated in Central America, which is where they reach their greatest extant diversity (Curson et al. 1994). Thus, it is best to think of them not as temperate birds that fly south to avoid starvation, but as tropical birds that fly north to nest in regions with fewer predators and a seasonal abundance of insects.

[22] In a paper characterizing ethology as a biological science, Tinbergen (1963) offered four distinct questions one can ask about biological phenomena, and which an ethologist can ask about behavior: What is its function? How does it develop? What is its adaptive significance? How did it evolve? Tinbergen does not cite Mayr, though they both cite Huxley as a prior inspiration. And while Tinbergen

In short, proximate causes explain the mechanisms of an individual and its interaction with its environment (including its development from a fertilized zygote to death, or from lag-phase to death-phase in asexual single-celled organisms), while ultimate causes explain *why* an individual develops and interacts with its environment in the way that it does and not in another way. The proximate-ultimate distinction has become a canonical element in biology and can be found in most introductory chapters of evolutionary biology, and in biology textbooks more generally (e.g., Futuyma and Kirkpatrick 2017, 7; Breed and Moore 2016, 2). Some even regard the paper in which Mayr introduces the distinction as being the "epistemological statement of the modern synthesis" (Dickins and Barton 2013, 748).

5.3 Two Arguments Against the Proximate-Ultimate Distinction

While the proximate-ultimate distinction has become a canonical element of introductory textbooks on evolutionary biology, it has not been without its critics (e.g., Ariew 2003; Amundson 2005; West-Eberhard 2003; Laland et al. 2009, 2011, 2013a, 2013b; Uller and Laland 2019). All these of these authors take the distinction between proximate and ultimate causes to be either purposively (e.g., Uller and Laland 2019) or inadvertently (e.g., West-Eberhard 2003) equated with a distinction between developmental and evolutionary causes. These authors thus take the distinction to entail a separation between those causes that explain developmental trajectories and those that explain evolutionary trajectories.[23] A further assumption that is made by some of these critics concerns their projection of Mayr's own views on the causal structure of development and consequently on proximate causes:

> Indeed, when Mayr described genetic causes as ultimate causes, despite that genes exercise their phenotypic effects through development, it reflected his

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added development (ontogeny) to Huxley's tripartite framework (causation, survival, and evolution), Mayr (1961) seems rather to have refined Huxley's view into a more general account of causation in biology. While there is significant overlap between Tinbergen and Mayr, I will not discuss Tinbergen further here.

[23] A brief caveat is needed here. In this context, development is understood inclusively, as all processes occurring to or initiating from/ in an organism during its life cycle. Thus, behavioral phenomena and individual ecological interactions are seen as developmental processes.

> metaphysical view of development as the execution of a genetic program (e.g., Mayr 1961, 1984). (Uller and Laland 2019, 5)

Let's, for the sake of argument, for the moment agree that Mayr takes development as the execution of a predetermined genetic program. In other words, Mayr gives causal and informational privilege to genes in the causal structure of development. This view is often referred to as genetic determinism, or in a less radical version, gene centrism. On this view, development (and sometimes even all phenotypic expression—even behavior such as nest-building or migration, e.g., Dawkins 1976, 1982, 2004) is predetermined by a genetic program which itself has been formed by generations of selection episodes that meticulously put together a program that is capable of producing the appropriate phenotypic expressions for the given environmental context. On such a view, then, proximate causes—those that govern the individual's development, physiology, and environmental interactions—are the products of a genetic program, which itself is a product of ultimate causes (primarily selection). Consequently, proximate causes cannot be causally efficacious in bringing about evolutionary outcomes, as proximate causes are the products of the prior action of selection on deterministic genetic programs which execute them.

5.3.1 The Causal Parity Argument (Argument from Constructive Development)

It is now well established that an organism's environment affects development via environmental conditions influencing pathways of gene expression, either directly or mediated through physiological effects (Nijhout 2003; Lewontin 2000; Gilbert 2012). This means that a genotype—or the genetic program—will produce different phenotypes in different environments. Such phenotypic plasticity has over the last few decades been extensively documented (West-Eberhard 2003; Sultan 2015; Gilbert and Epel 2015) across many types of organisms and in relation to a diversity of environmental conditions (Sultan 2019). Thus, the phenotype is *underdetermined* by the genotype. There are several more causal factors involved in shaping developmental trajectories than just a series of gene expressions. For example, developmental pathways can be triggered by specific environmental cues, such as the temperature-dependent sex determination in reptiles (Warner and Shine 2008) or by environmentally induced epigenetic changes to gene functions (John and Rougeulle

2018). The underdetermination of the phenotype, the multiple sources of developmental information, and many different causal factors involved in development was summarized by proponents of developmental systems theory in the causal parity thesis (e.g., Oyama 2000; Oyama et al. 2001; Griffiths and Gray 1994). This was intended as a challenge to genetic determinism and more generally gene-centric views of ontogeny and phylogeny—the view that genes play a special and privileged role in development and evolution (Kjosavik 2014). Building on the insights of developmental systems theory, as well Lewontin's constructionist biology (e.g., Lewontin 1983a, 2000), Laland et al. (2015; 2019) and others (e.g., Moczek 2019) offer an alternative to viewing development as the execution of a genetic program, which they call *constructive development*. According to this view, developmental processes are to be regarded as:

> Open and constructive through self-assembly, and a corresponding rejection of the idea that organisms and their activities are fully specified by genetic programs. Organisms are regarded as influenced, but not determined, by their genes, and their activities as shaped by developmental information-gaining processes as well as natural selection acting on genetic variation. (Laland et al. 2019, 132-133)

In relation to the proximate-ultimate distinction, this view features as a central premise in the causal parity argument (or the argument from constructive development). This can be formulated as follows:

P1. The distinction between proximate and ultimate causes is equal to the distinction between developmental processes and evolutionary processes (*identity assumption*).

P2. If development processes are simply the execution of genetic programs shaped by the prior action of selection, then developmental causes cannot be causally efficacious in evolutionary trajectories or outcomes. (*gene-centrism*)

P3. Developmental processes are not simply the execution of genetic programs, but rather an open and constructive process (*the causal parity thesis/ constructive development*).

C1. Developmental processes are not, in principle, causally inefficacious in producing evolutionary outcomes or influencing evolutionary trajectories.

If we take Mayr to hold that the causal structure of development consists primarily in the execution of a predetermined genetic program that has been determined by the prior action of selection, and that he equated proximate causes with developmental causes and ultimate causes with evolutionary processes, then this argument hits its mark.

That, however, is a big if. While Mayr uses the metaphor of a program, both in the texts cited by Uller and Laland (2019) and elsewhere (e.g., Mayr 2001), it is still only a metaphor which is invoked in order to talk about goal-directed processes—such as development—which themselves are products of natural selection. The metaphor does not entail that the execution of such programs is completely determined by the prior action of natural selection. Mayr surely knew that different environmental stimuli may affect an organism's development and ecological interactions, as he was keenly aware of the differences in learned and instinctual behavior. In relation to behavior, Mayr (1974) even argued that selection can favor either open or closed behavioral programs, in which open programs modify outcomes based on experience and closed programs change outcomes little or not at all based on experience. Static and homogenous environmental conditions tend to select for closed behavioral programs, while dynamic and heterogenous environmental conditions favor open behavioral programs. Thus, in cases in which behavior is in fact executed by predetermined genetic program, there is good reason for that. These are cases in which open programs have been outcompeted by closed ones. In the case of open behavioral programs—which might be the norm—the behavior (viz., the execution of the genetic program) is *not* predetermined by natural selection, but rather sensitive to experience and environmental stimuli.

A similar response in relation to phenotypic plasticity and constructive development more generally is to conceive of the *extent of phenotypic underdetermination* (i.e., the possibility of plastic responses to the environment—usually referred to as the *norm of reaction*) as a variable trait that is under selection (e.g., Dewitt and Scheiner 2004). On such a view, developmental processes can be influenced by environmental conditions, yet the ultimate explanation of such environmentally induced developmental responses is by reference to the prior selection on different reaction norms, which are themselves seen as a self-contained "property of the genotype" or as an "environmental response program of the genes" (Nager, Keller, and Van Noordwijk 2000; de Jong 1999, see Sultan 2019, 110 for discussion). The point is, for phenotypic underdetermination to be available to selection, and consequently shape evolutionary outcomes, it needs to be something that varies amongst individuals in a population. It further needs to provide a competitive advantage in relation to other members of the population (i.e., increased relative fitness). This point is succinctly summarized by Dickins and Dickins (2018):

> The developmental processes that build a phenotype only provide antecedent conditions for a bout of selection; there must be something that varies and that can be differentiated through competition. Thus, put crudely, if some environmental condition arises such that individuals that develop an aspect of their phenotype in a particular way thrive relative to others that cannot develop in this way, selection will favour the former. This is all about individual differences in the developmental response, something captured by the concept of reaction norms in biology. (Dickins and Dickins 2018, 164)

Thus, the argument that Mayr uses of the metaphor of a genetic program entail genetic determinism is simply false. Further, merely pointing out that genotypes are underdetermined by their phenotypes, and that development is not simply an unfolding or execution of a predetermined genetic program, does not really challenge the proximate-ultimate distinction. Even if we, for the sake of argument, grant the identity assumption, plastic responses can still be treated as variables traits under selection—namely as reaction norms.[24]

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[24] A qualificatory statement might be useful here. Selection cannot act on latent phenotypic expression directly, it is an ecological process and acts on the actual phenotypes produced by the reaction norm of each individual genotype. Thus, while the variation available to selection are different phenotypes, what is responsible for the expression the appropriate phenotype in the next generation and in the particular environmental context is the inheritance of similar reaction norms from parent to offspring. Thus, while there is *selection-for* actual phenotypes, there might be *selection-of* reaction norms with different ranges of phenotypic expression, if for example, there is stable and predictable environmental heterogeneity. Even if, as some suggest, reaction norms are not appropriately attributable to the genotype (i.e., conceived as genotype-environment interaction), but rather to a genotype-phenotype-environment interaction (e.g., Sultan 2019), the point still stands. There must be heritable (not necessarily genetic)

However, something that might be more problematic for the proximate-ultimate distinction is the potential role phenotypic plasticity can play as a source of evolutionary *innovation* and *novelty* (e.g., Moczeck et al. 2011). These authors argue that an adaptive plastic response to changing environmental conditions can subsequently be refined and stabilized as traits under strong genetic control through genetic accommodation or assimilation (Baldwin 1896a, 1896b; Waddington 1953; West-Eberhard 2003; Sultan 2015). On this view, often called "plasticity-first" evolution (Levis and Pfenning 2016), "genes are followers, not necessarily leaders, in phenotypic evolution" (West-Eberhard 2003, 158). Such cases may be more problematic for the proximate-ultimate distinction, as they are cases in which developmental processes are both the sources and drivers of adaptation (Laland et al. 2013a, 2013b; Bateson 2017a, 2017b; Bateson and Gluckman 2011). In these cases, proximate causes influence ultimate events, something which is inconsistent with a separation of proximate and ultimate causes, when identified with developmental and evolutionary processes respectively.

However, it is not clear that we should identify proximate and ultimate causes with developmental and evolutionary processes. In section 5.4 we shall see that the there is little reasons to hold on to the identity assumption. Further, I take the challenge offered by "plasticity-first" evolution to the proximate-ultimate distinction as an instance of the causal incompleteness argument which we shall turn to next.

5.3.2 The Causal Incompleteness Argument (Argument from Reciprocal Causation)

The second challenge to the proximate-ultimate distinction concerns (primarily) cases of reciprocal causation. These are instances in which explanations of evolutionary outcomes are incomplete without accounting for the sources and origins of selection pressures—or the origins of novel phenotypic variation—and where such an account invokes proximate causes (Laland et al. 2013a, 2013b). Paradigmatic instances of reciprocal causation can be found in cases of *niche construction*.[25] Niche construction,

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variation in plastic phenotypic expression in response to different environmental factors amongst the individuals of the population in order for selection to produce an evolutionary outcome.

[25] Reciprocal causation is argued to be widespread, and instances can be found not only with niche construction, but also in cases of coevolution, sexual selection (e.g., mate-choice theory), frequency-dependent selection, social evolution, maternal effects, and so on. See Laland et al. (2009, 2011, 2013a,

as we have seen in the preceding chapters, occurs when organisms actively modify their environment or relationship to it, such that the selective environment is changed (Odling-Smee et al. 2003; Laland et al. 2016).

The soil-processing effects of earthworms provide a good illustration of the challenge to the proximate-ultimate distinction offered by the argument from causal incompleteness (or reciprocal causation). Through their burrowing and related activities (e.g., eating and excreting), earthworms alter the biological, chemical, and physical characteristics of the soil to the benefit of many other species—especially plants—since earthworms boost soil fertility. Earthworms are thus responsible for modifying some environmental variables that are parts of the selective environment of other species—the proximate activities of earthworm can influence ultimate events (Laland et al. 2005, 2019).

In addition to affecting the selection pressures on other species, earthworm behavior affects the selection pressures of its own species, primarily through lowering of the soil matric potential (the amount of energy it costs to extract water from the soil), which helps the earthworms avoid desiccation in their relatively dry terrestrial habitat (Turner 2000). The earthworm is physiologically quite poorly adapted to terrestrial life. The organs that serve the same function as kidneys in vertebrates, the *nephridia*, do not store water, leading to a daily water loss of 60-90% of its bodyweight. Daily water loss for humans, by contrast, is 2,5-10%. If earthworms resided in a freshwater aquatic habitat, this would not be a problem. In fact, it would be adaptive since the main challenge in such a habitat is to conserve internal solutes and other minerals during constant diffusion of water through the body. While there is an advantage to urinating large amounts of diluted urine with low solute concentration in freshwater aquatic habitats, this is not the case for terrestrial habitats. Under such circumstances, organisms should produce low quantities of urine with a higher solute concentration (Turner 2000).

Earthworms thus transform the soil they are living in, making it more suitable for their own physiology by lowering the soil matric potential such that water is easier to obtain (and retain) from their physical surroundings. The altered soil is passed on to

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2013b) and Uller and Laland (2019) for a more in-depth discussion of these examples. However, it is not clear that evolutionary theorists do not incorporate reciprocal causation into their models whenever they are able to. See, e.g., Svensson (2018).

the subsequent generations through ecological inheritance. This is thus a form of niche construction that involves trans-generational adaptive modification of the environment, which in turn has selective effects.

An important consequence of niche construction for evolutionary dynamics is that it generates feedback between organismic activities and environmental conditions. The fact that organisms can inherit modified ecological conditions through ecological inheritance is what makes this feedback particularly interesting, as it constitutes a reciprocal relationship between the activities of an organism and the environmental states which are affected by those activities over generations. This reciprocal relationship can have strong effects on subsequent evolution (Laland et al. 2005).

In the earthworm example, the ultimate explanation of the trait of the earthworm—the retention of the nephridia adapted for a freshwater habitat—is explained by the environmental conditions of the earthworm. In particular that they primarily interact with soil that have a relatively low matric potential. However, the environmental conditions themselves—soil with low matric potential—are explained in part by the activities of individual earthworms over generations. Thus, an evolutionary explanation of the nephridia retention is *causally incomplete* without a reference to the proximate causes—the burrowing activities of individual earthworms—which maintain the selective environment over generations. A general version of the argument from causal incompleteness can be formulated as follows.

P1. The distinction between proximate and ultimate causes is equal to the distinction between developmental processes and evolutionary processes (*identity assumption*).

P2. If evolutionary outcomes are sufficiently explained by ultimate causes alone, then proximate causes are not involved in evolutionary outcomes (*causal exclusion assumption*).

P3. In many cases, evolutionary outcomes cannot be fully explained without a reference to proximate causes (*reciprocal causation and "plasticity-first" evolution*).

C1. Many evolutionary explanations that only invoke ultimate causes are *causally incomplete* explanations.

Like the causal parity argument, the causal completeness argument depends on the identity assumption. However, we shall grant this assumption for now and rather look at another problematic premise. In P2 there is a conflation of *causal incompleteness* with *explanatory adequacy* (Scholl and Pigliucci 2015). We rarely, if ever, provide causally complete explanations. Rather causal explanations are adjusted to context. As Dretske (2013) points out:

> Causal explanations are context sensitive. What we pick out as the cause of *E* in causal explanations of *E* depends on our interests, our purposes, and our prior knowledge. Almost any event *E* depends on a great variety of other events in such a way as to make any one of them eligible, given the right context, as the cause in causal explanations of *E*. (Dretske 2013, 139)

Evolutionary explanations are no different. While there is a complex causal web of causal processes leading up to, say, the evolution of migration in a population of warblers, the job of the evolutionary biologist (studying the ultimate causes) and the functional biologist (studying proximate causes) is to pick out the significant causes for their research context. So, the claim that since proximate causes do not feature in evolutionary explanations, then they must be causally inefficacious in evolutionary events is false. The claim in P2 should rather be interpreted as a claim about evolutionary *explanations*, and not evolutionary *causes*. A more charitable way of reading P2 is as saying that to explain evolutionary outcomes, only ultimate causes are needed, and proximate causes can be treated as background conditions. In evolutionary explanations, the explanatory bread and butter are changes to populations over generations and the processes that bring about that change. Thus, including causes at the level of the individual organisms might not be appropriate for the context of the research question. However, this does not mean that individuals are not causal participants in the evolutionary theater. As we saw in chapter 1, Mayr (2001) holds that individuals are in fact central to evolutionary theory in virtue of being the principal object of selection:

> Evolution deals with phenotypes of individuals, with populations, with species; it is not "a change in gene frequencies." The two most important units in

> evolution are the individual, the principal object of selection, and the population, the stage of diversifying evolution. (Mayr 2001, xiv-xv).

Clearly, what an individual does during its lifetime might influence its realized fitness (viz., causally influence evolutionary outcomes), whether this is brought about by plastic responses to environmental heterogeneity, learning, gene expression, or chance events. Even in Mayr's original example, the migration of the warblers of New Hampshire, it was (presumably) individual warblers that initiated travelling further North from their native tropical habitat of Central America during interglacial periods in search of seasonal resources (Curson et al. 1994). However, when we want to explain *why* the warblers of New Hampshire have ended up being migratory, we are asking what processes led them to migrate and not remain a sedentary tropical species (alternatively explaining why the warbler migrates south in winter and not opt for a sedentary ecological lifestyle in New Hampshire, as in Mayr 1961). The overarching explanation is, presumably, that some New World Warblers native to Central America started travelling North during warmer interglacial periods and in doing so constructed a new niche—Northern summer migration—which was consequently been maintained and refined by natural selection.

The question "why do warblers migrate?", however, does not pertain to these individual warblers. In fact, it is not a question that is asked of individual warblers at all, nor can it be satisfactorily answered by referring to the action of individuals. It is a question asked of a population and we must answer it by invoking causes that bring about changes to populations. Although it might have been initiated by the habitat choice (or relocational niche construction) of some individual warblers, it is in virtue of natural selection favoring migratory warblers, and consequently eliminating sedentary ones, that the warblers of New Hampshire migrate. And it is by specifying *why* natural selection favors a migratory lifestyle, and not alternative ecological lifestyles, that we provide ultimate explanations.[26] In other words, while ultimate

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[26] There are (at least) two different selective environments which can be invoked to account for this. On the one hand, we have the possibility of migratory warblers attempting a *Central American* sedentary lifestyle. In this case, since there is the greatest extant diversity of New World Warblers in Central America, it will presumably be interspecies competition for sedentary niches. Consequently, the selective environment might favor a migratory lifestyle as a response interspecies competitive exclusion. In the case of a *North American* sedentary lifestyle, the selective environment will probably favor a

explanations do not include proximate causes, this does not mean that developmental or other individual-level processes are inconsequential to evolutionary outcomes. It just means that unless those developmental processes engender changes at the level of populations, they are often best regarded as acting in the background of evolutionary processes when providing evolutionary explanations.

5.3.3 The Explanatory Indispensability Argument

The proponent of the causal incompleteness argument can respond by adjusting its target. Instead of arguing that the distinction between proximate and ultimate causes leads to developmental processes being excluded from the causal story of evolutionary outcomes—which as we have seen above, it doesn't—they can argue that it still leads to an *explanatory incompleteness*. This seems to be the strategy of Laland et al. (2019), who argue that many evolutionary explanations in which only ultimate causes are provided, and the activities of indvidual organisms are ignored, leave an *explanatory gap* (Laland et al. 2019, 127-133). These are cases in which individual-level (developmental) causes are needed to provide a satisfactory explanation of an evolutionary outcome. For many of the instances in which there exists reciprocal causal relationships between an organism's activity and their selective environment, this will be the case. For example, in the case of the earthworm above, it is the burrowing activities of individual earthworms that maintain a selective environment in which an osmoregulatory organ adapted for an aquatic lifestyle is not eliminated. So, if we ask the ultimate question "why does the earthworm retain nephridia adapted for an aquatic lifestyle as their osmoregulatory organ?", then it seems that the burrowing activities of individual earthworms are *explanatorily indispensable causes*. We can thus formulate an argument from *explanatory indispensability*.

P1. The distinction between proximate and ultimate causes is equal to the distinction between developmental processes and evolutionary processes (*identity assumption*).

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migratory lifestyle as opposed to a sedentary lifestyle due to resource scarcity and challenging abiotic conditions (e.g., low temperatures) during winter months.

P2.* If evolutionary outcomes are sufficiently explained by ultimate causes alone, then proximate causes are explanatory dispensable in explanations of evolutionary outcomes (*explanatory dispensability assumption*).

P3. In many evolutionary explanations proximate causes are *explanatory indispensable* (e.g., reciprocal causation and "plasticity-first" evolution).

C1. Many evolutionary explanations that only invoke ultimate causes are *explanatory incomplete* explanations.

This argument is similar to the causal incompleteness argument, only that P2* has been changed from being a claim about evolutionary *causation*, to being a claim about evolutionary *explanations*. I think many will agree that there are evolutionary explanations in which individual-level processes, either developmental, ecological, or behavioral, are *explanatory indispensable*. The earthworm example strikes me as a compelling example, as might cases of the Baldwin effect, behavioral innovation, "plasticity-first" evolution, etc. But does this argument undermine the proximate-ultimate distinction? There are (at least) two reasons why I think it fails to do just that. First, the elephant in the room, the identity assumption. Are there good reasons for why we should hold that proximate and ultimate causes should be equated to developmental and evolutionary processes? If we do not, then all the arguments against the proximate-ultimate distinction break down. Second, it is not in virtue of being individual-level processes that the activities of earthworms are explanatory indispensable, rather it is in virtue of their influence on population-level processes, specifically how it influences the action of natural selection. Let's begin by looking at the identity assumption.

5.4 The Proximate-Developmental and Ultimate-Evolutionary Conflation

A central motivation for Laland et al. (2011, 2013a, 2013b) and Uller and Laland (2019) for undermining the proximate-ultimate distinction is to allow more causal factors to figure in evolutionary explanations (Laland 2015). Most of these causal factors are (at first glance) individual-level processes occurring during an organism's development. Thus, when Mayr distinguishes between the proximate causes studied by the functional biologist and the ultimate causes studied by the evolutionary biologist, and argues that ultimate causes can be divided into *genetic* (accounting for genetic programs responsible for development) and *ecological* causes (accounting for the selection for genetic programs that perform better than others), it might seem natural to think that the proximate-ultimate distinction correspond neatly with developmental-evolutionary distinction.

However, a more charitable way of interpreting the distinction between genetic and ecological ultimate causes is to view them as *variational* and *eliminatory* causes. The variational causes are those which contribute heritable phenotypic variation to the population. In many cases, this will be different genotypes that express different phenotypes. In other cases, this could be plastic responses, learned behaviors, or behavioral innovation. As long as those phenotypic traits are heritable—not necessarily only through genetic inheritance—and engender fitness differences, then they can be acted on and maintained by natural selection. The eliminatory causes—or ecological causes—are best understood as the selection pressures that directs the action of selection in a particular evolutionary episode (viz., those that eliminate unfavorable variants). Whether these are caused be purely external abiotic environmental factors (e.g., temperature, day-length, etc.) or by organismic activities (e.g., earthworm burrowing) is inconsequential to the action of selection. Conceived as such, Mayr's genetic and ecological ultimate causes are simply those that cause there to be directional differential reproduction in a population due to heritable fitness differences. Thus, we can treat proximate causes as those that explain *how* an individual interacts with its environment (including ontogeny), while ultimate causes are those that explain *why* the organism interacts the way it does, and not in another way (Scott-Phillips et al. 2011; Futuyma and Kirkpatrick 2017). There is nothing on this interpretation of proximate and ultimate causes that implies an identification with developmental and evolutionary causes, or a concomitant exclusion of either in their respective explanations. In fact, Mayr himself (1960, 1963) seems to undermine such a identification.

5.4.1 Mayr's Pacemaker Model and Niche Construction

In discussing evolutionary novelty, Mayr argues that behavior often play the role of a "pacemaker" whereby behavior frequently exposes organisms to novel selection pressures which can result in relatively rapid subsequent evolutionary changes in life history, morphological, and physiological traits (Duckworth 2009):

> A shift into a new niche or adaptive zone is, almost without exception, initiated by a change in behavior. The other adaptations to the new niche, particularly the structural ones, are acquired secondarily (Mayr 1958, 1960). With habitat and food selection—behavioral phenomena—playing a major role in the shift into new adaptive zones, the importance of behavior in initiating new evolutionary events is self-evident. (Mayr 1963, 604)

It is clear from this that Mayr would be sympathetic towards developmental causes being a part of the causal history and explanation of evolutionary events. As we can see from the quote above, for Mayr an individual organism can actively participate in its own evolution in virtue of initiating an evolutionary event through its behavior. There are some striking resemblances between Mayr's "pacemaker" model for evolutionary shifts and novelties and much of the work which is citied to undermine the proximate-ultimate distinction collectively referred to as instances of reciprocal causation and "plasticity-first" evolution. As Svensson (2018) points out:

> Mayr's view of a crucial role of behaviour in the evolutionary process is clearly compatible with feedback between the organism and its environment. Mayr's surprisingly early insights on the issue has clear similarities with similar views expressed several decades later by West-Eberhard, Levins and Lewontin (West-Eberhard 1983; Levins and Lewontin 1985), albeit not developed in detail by him. (Svensson 2018, 6)

Further, what is referred to as *relocational* niche construction (whereby organisms move in space and consequently alter the environmental factors they interact with, Odling-Smee et al. 2003) and *experiential niche construction* (whereby organisms alter how they experience their environment through behavior, Sultan 2015; Chiu 2019)[27]

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[27] Including plastic responses which alter morphological characters. For example, some plants alter leaf size and shape in relation to the availability of light in their environment such that the plant's experience a higher (or lower) photon-density (Sultan 2015). We will revisit this example, as well as the different kinds of niche construction in chapter 6 and 7.

would, if they result in evolutionary changes, all be instances of Mayr's "pacemaker" model for evolutionary shifts and novelties initiated by behavior or phenotypic plasticity.

Thus, it seems unlikely that the identity assumption is something which Mayr himself would agree with. Further, a more charitable interpretation of what proximate and ultimate causes refer to, namely those pertaining to the individual organism and its ecological and developmental context (proximate), and those that pertain to changes at population-level (ultimate causes), seem to better reflect the original motivation behind the introduction of the proximate-ultimate distinction.

5.5 Structuring and Triggering Causes and the Proximate-Ultimate Distinction

I hope now to have shown that neither the causal parity argument, causal completeness argument, nor the explanatory indispensability argument successfully undermine the proximate-ultimate distinction. However, in the following section I want to offer a way to conceive of the distinction between proximate and ultimate causes that allows for instances of reciprocal causation and non-genetic novel phenotypic variation to be conceived of as ultimate causes, and consequently figure in explanations of evolutionary outcomes. I will do so by invoking the distinction between structuring and triggering causes. The structuring-triggering cause distinction is borrowed from Dretske (1988, 2004). It is not a distinction he originated, but is nicely formulated by him through a thought experiment:

> A terrorist plants a bomb in the general's car. The bomb sits there for days until the general gets in his car and turns the key to start the engine. The bomb is detonated (triggered by turning the key in the ignition) and the general is killed. Who killed him? The terrorist, of course. How? By planting a bomb in his car. Although the general's own action (turning on the engine) was the triggering cause, the terrorist's action, wiring the bomb to the ignition, is the structuring cause, and it will surely be the terrorist's action, something that happened a week ago, that will be singled out, in both legal and moral inquiries, as the cause of the explosion that resulted in the general's death. (Dretske 2004, 169)

This distinction has already been used to analyze causes in evolutionary biology, in particular in the debates as to whether fitness differences, selection, and drift can be causes of evolution (Ramsey 2016). In arguing that selection or fitness is a cause, it needs to be established what sort of causes they are. Ramsey (2016) invokes the structuring-triggering cause distinction to argue that while fitness difference might not be a triggering cause of evolutionary outcomes, it is can be seen as a structuring cause.

To better see how the structuring-triggering cause distinction translates to biological causes, it is helpful to consider organismic life histories. A life history is an entire life lived by an organism. It has various properties, some are common and periodic (being asleep), some persist until death once they arrive (being adult), others are ephemeral (eating a particular meal at a specific moment). What is most relevant to selection, fitness, and drift are special events along the life history, namely, acts of reproduction (and events influencing the prospects of reproduction)—in particular, the quantity and timing of reproductive acts distributed over life histories. In this framework, fitness can be understood as a disposition, which could be fleshed out in terms of the average[28] reproduction over the set of life histories, not just actual life histories but possible life histories. But of these possibilities, of course, only one life is lived. The life that is lived is *triggered* by the specific set of circumstances encountered by the organism. But the entire set of life histories is *structured* by the characteristics of the organism and the totality of the environmental variables.

Let's now consider how the distinction structuring causes map onto the distinction between proximate and ultimate causes. Picture again the set of possible life histories that an organism might follow. Take the example of a bird, a robin, say, beginning as an egg deposited in a nest. This robin has many possible lives before it. It may die young, perhaps just after fledging, or perhaps a year into its life. It might succumb to starvation, disease, predation, or an accident. We can ask of an individual what triggered the life that it lived. And we might wonder why it had the outcome it did instead of another. Why did it starve while its nestmates survived? Asking why an individual followed one among the possible life histories is to ask about the triggering causes.

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[28] An average—understood as an arithmetic mean—is not, it turns out, the best way of quantifying fitness. See Pence and Ramsey (2013) for a discussion of the mathematical foundation of fitness.

How are proximate causes related to triggering causes? To answer this question, consider again the terrorist example with additional complexities added by Ramsey (2016):

> It could be that the terrorist did not want to blow up the general's family, so she put a pressure sensor under the back seat that would make the key trigger only a secondary smoke bomb intended to warn and to terrorize him and his family. A single structuring cause (setting up the car with the pair of bombs, the pressure sensor, and the key switch) has set the world to have two possible outcomes (assuming, of course, that the general will definitely turn the key). (Ramsey 2016, 432)

In such a situation, we can ask about the possible outcomes for the general, and we can ask why one among the possible outcomes was triggered. These questions become more interesting if we have a population of like individuals, as we do in biological species. If we ask of the population why it evolved in a particular way over some stretch of time, we will be interested in structuring causes, since those are the causes that determine the characteristics of the set of possible life histories. It is this set of possibilities that is important, and the exploration of this possibility space by the population has evolutionary consequences.

The world is set up such that most robin life histories end prior to successful reproduction—indeed, most die in their first year (e.g., Sullivan 1986; Yackel-Adams et al. 2006). There is thus an incredible selection pressure during this first year on being able to procure sufficient food and avoid succumbing to parasites or predators. These pressures shape the possibility space; they are structuring causes. And it is these causes that we examine in understanding evolution.

Nevertheless, just as we can ask what it was that triggered the smoke bomb in the general's car instead of the fatal bomb, we can ask of an individual robin what it was that triggered the life outcomes that it realized. Why did this robin live only a week after fledging? What triggered this life history instead of other possibilities, such as bearing broods in two successive seasons before succumbing to predation? Thus, we have two questions: First, why does the set of possible life histories for this population (or species) have the characteristics that it does? Second, why did this individual follow this particular life history instead of another possibility? The first is answered in terms of structuring causes, the second in terms of triggering causes. Structuring causes thus do the job of ultimate causes, they explain why a population of organisms have the characteristics they have and not others, while triggering causes can do the job of proximate causes by explaining how (through which mechanisms) a particular organism interacts with its environment or how it develops.

5.6 Reciprocal Causation and Phenotypic Plasticity as an Ultimate Cause

In the preceding section I offered the rationale behind interpreting ultimate causes as structuring causes and triggering causes as proximate causes. Now I want to show how on such an interpretation, ultimate causes can include individual-level processes in virtue of those processes engendering population-level changes. Let us revisit the earthworm example. In that case the joint effect of individual-level burrowing activities creates a selective environment in which the population-level response is to retain a *nephridia* adapted to an aquatic, and not terrestrial, environment. As we saw above, a proper explanation of *why* the earthworm retains the *nephridia* invokes the action of selection, but the action of selection cannot be fully appreciated without an account of what generate and maintain the selection pressures which produce the adaptive response. In this case, the ultimate cause of the nephridia retention is the action of natural selection. However, the action of selection is *structured* by the activities of the earthworms. As such, the joint effect of individual-level burrowing activities is *what causes* natural selection to favor nephridia retention. In Mayr’s vocabulary, the individual-level burrowing is the (*ultimate*) *ecological* cause of the nephridia retention. However, it is not in virtue of being an individual-level process that the burrowing activity is an ecological cause, but rather in virtue of the joint effect all the burrowing activities have on the action of natural selection. In this case, the burrowing activity has the same explanatory validity as other abiotic and biotic environmental factors in evolutionary explanations. For example, why did melanism spread in peppered moth populations across Britain in the 1800s? The ecological cause is the increased presence of soot on resting surfaces made the grey morph more conspicuous. The presence of soot thus *structured* the action of selection to favor melanistic morphs.

Next, let see how non-genetic phenotypic novelty and innovation (e.g., “plasticity-first” evolution, behavioral innovation, habitat choice, learning) can be an ultimate cause in evolutionary explanations. In these cases, novel phenotypic expression of a single individual can produce an adaptive response which subsequently is distributed in the population and thus engender evolutionary change.[29] As an example, let's imagine a Macaque which discovers that it can use a rock to crush the shell of clams easily foraged at the seashore. Let's further imagine that the clam-crushing Macaque enjoys a significant fitness advantage in virtue of the extra calories of protein and fat the clam provides, relative to other the non-clam-crushing members of its population. Let's also say that the behavior is only transmitted through parent-offspring teaching. If the fitness advantage is great enough and the fidelity of the parent-offspring learning is high enough, the clam-crushing behavior will spread rapidly in the population through directional selection. In this example, there is behavioral innovation (a case of non-genetic phenotypic novelty), which is transmitted vertically through parent-offspring learning. In such a case there are two ways that the clam-crushing innovation acts as an ultimate cause. First, the behavioral innovation introduces novel heritable variation for selection to act on. In this sense it is similar to what Mayr calls a *genetic* cause in an ultimate explanation—which I called a variational cause. The novel variation structures the action of selection in virtue of providing a new factor to select for. Provided that the clam-crushing behavior confers a great enough fitness advantage, and the techniques is transmitted with high fidelity, the distribution of clam-crushing behavior will spread in the population and thus cause evolutionary change. Second, the clam-crushing behavior also creates novel selection pressures such as the capacity for learning/teaching, finding the right size and shape of rock, manual dexterity, and so on. Thus, not only did the behavioral innovation act as an ultimate cause in virtue of generating novel heritable phenotypic variation—i.e., as a *genetic* ultimate cause. Amongst the clam-crushing individuals, there will be selection for the proficiency in learning and mastering of the skill of crushing clams. Thus, when the individual-level behavior has spread in the population, the behavior also becomes an *ecological* ultimate cause.

By interpreting the proximate-ultimate distinction as a distinction between structuring and triggering causes, we can see how individual organisms can contribute

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[29] At least on Mayr's (2001) view of evolution as the changes in the phenotypes of a population, and not necessarily the genotypes.

to evolutionary outcomes by structuring the action of population-level processes or otherwise influence (viz., structure) population-level outcomes.

5.7 Conclusion

In this chapter I showed how two arguments offered to undermine the proximate-ultimate distinction do not hold. These arguments are provided to justify individual-level developmental processes and behaviors in playing an explanatory role in accounting for evolutionary outcomes. The implication being that this is not possible with a distinction between proximate and ultimate causes. I offered an alternative interpretation proximate and ultimate causes—as triggering and structuring causes. On this view, individual-level processes can act as ultimate causes in evolutionary explanations in virtue of structuring population-level causes or otherwise influence population-level outcomes.

6

THE CAUSAL STRUCTURE OF NICHE CONSTRUCTION THEORY

6.1 Introduction

The asymmetrically externalist conception evolution by natural selection, as we have seen, take the environment to pose problems for organisms, and that those problems act as selection pressures, which consequently engender to adaptive evolutionary responses. This view thus regards the environment as an external initiator and prime cause of adaptive evolution (Barton and Partridge 2000; Williams 1966). From the preceding chapters it is clear that this view is increasingly being called into question. One important argument that challenge the asymmetrically externalist picture of evolution by natural selection stems from *the niche construction perspective*. This approach takes organisms to be not merely, or not always, passive recipients of environmental challenges (Lewontin 1983b; Levins and Lewontin 1985; Piaget 1978; Laland *et al*. 2000). Instead, organisms can take an active role in their evolutionary fate (Odling-Smee 2010; Odling-Smee *et al*. 2003; West-Eberhard 2003). One way of doing so is by moving around or actively changing themselves or their environment, thereby changing the selection pressures acting on them. This active modification of selection pressures by organisms has been labeled ‘niche construction’ (Odling-Smee 1988).

The niche construction perspective thus grew out a dissatisfaction with how evolutionary biology standardly explained adaptation (Lewontin 1978, 1991, 2000; Levins and Lewontin 1985; Godfrey-Smith 1996; Odling-Smee 1988; Odling-Smee *et al.* 2003). This dissatisfaction led to critiques centered on the asymmetrically externalist character of the standard view, which, as we have seen, takes organismic adaptations to be explained by environmental properties, while the environmental properties are explained by other sets of properties internal to the environmental system (Godfrey-Smith 1996, Odling-Smee 2003; see chapter 4). Williams (1992) is often quoted in characterizing this view:

> Adaptation is always asymmetrical; organisms adapt to their environments, never vice versa. If the environments at the surface of the Earth seem well suited to living organisms, it is simply because those are the environments to which the organisms have adapted. (Williams, 1992, 484)

Lewontin (1983; Levins and Lewontin 1985) and Odling-Smee (1988) argued early on that in many cases, organisms construct their own niches, and their adaptive fit cannot be explained solely with reference to an environment selecting for the organisms that happen to best deal with the environmental problems at hand. Indeed, Lewontin (2000) argued that the metaphor of adaptation should be replaced because it carries externalist implications. As the word ‘adaptation’ stems from the Latin word ‘adaptare’—which means ‘to make fit’—the implication, according to Lewontin, is that the organism is made to fit into a pre-existing ecological niche (Levins and Lewontin 1985). Lewontin offered an alternative to externalist adaptationism, which he called *constructionism* (Lewontin 1991). Lewontin argued that not only do organism influence the dynamics of the environment, but the environment itself has to be defined relative to an organism: “The environment of an organism is the penumbra of external conditions that are relevant to it because it has effective interactions with those aspects of the outer world” (Lewontin 2000, 48-9).

For Lewontin, the possible interactions an organism can have with its physical surroundings is what constitutes its environment. Consequently, the match between organism and environment is explained in terms of organism-environment interactions over time. On this view, organismic activity and reciprocal causation are explanatorily relevant for the explanation of adaptation. Godfrey-Smith (1996) calls these constructivist explanations of adaptation. Inspired by Lewontin,[30] Odling-Smee (1988) coined the term 'niche construction'. This term is supposed to pick out the process by which some organisms achieve an adaptive fit through their active modification of the conditions of the environment to better suit their lifestyle or morphology, and of the feedback that this modification generates. Niche construction is thus a causal process capable of generating an organism-environment fit and serves as an alternative interactionist explanatory structure, especially in cases where externalist explanations are inadequate or inappropriate, as we saw in chapter 4.

The concept of niche construction has generated some degree of controversy in evolutionary biology (Laland and Sterelny 2006; Scott-Phillips 2014). While no one denies that organisms are active and have certain effects on their physical surroundings, many are skeptical about the extent to which such effects can generate persistent and sufficiently strong feedback over generations to have an explanatorily relevant causal influence on evolutionary dynamics (Dawkins 2004). The divergent views on niche construction fall roughly into two interpretations:

The Supplementary Interpretation: Niche construction refers to a set of mechanisms (niche construction activities, reciprocal causation, and inclusive inheritance) that explain some cases of adaptation,[31] which are not included in the standard practice of selection-based explanations of adaptations (Godfrey-Smith 1996; Odling-Smee et al. 2003).

The Revisionary Interpretation: Niche construction refers to an evolutionary process that runs parallel to natural selection, and significantly alters the causal structure of evolution by directing or counteracting the action of natural selection (Laland 2015; Laland et al. 2017).

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[30] Schrödinger (1944) and Waddington (1969) are also important precursors to a more interactionist/constructionist approach to biology.

[31] Schulz (2014) points out that the relative frequency of niche construction explanations of adaptations seems to be the most controversial aspect of debates over the role of niche construction in evolutionary theory.

In chapter 4 I argued that niche construction is an example of a processes that can influence adaptive outcomes, but that conceiving of it as a process that runs in the opposite causal direction of natural selection inadvertently treats natural selection as an externalist, purely environmental, process. In this chapter, I will offer a framework for understanding and distinguishing distinct forms of niche construction in particular. This theoretical framework should be seen as an effort of conceptualizing niche construction and its place in evolutionary theory in line with the supplementary interpretation. Following the line of reasoning from chapters 3 and 4, I hold that there is nothing intrinsic to evolutionary theory which implies that natural selection acts only from the environment to the organism (in other words, natural selection is not exclusively an externalist process). If an organism solves—or dissolves—an adaptive problem by actively modifying the properties of itself or of the environment, or by modifying the way it interacts with the environment, natural selection will select for the traits involved in this modification (so long as there are not countervailing negative consequences). As we have seen, the two most important and controversial points that niche construction brings to the forefront of evolutionary theory—the active role of the organism in its evolution and how reciprocal causation affects evolutionary trajectories and alters our explanations of adaptations—are perfectly compatible with the principles of natural selection. What the niche construction perspective is not compatible with is an asymmetrically externalist reification of the principles of natural selection. Asymmetrical externalism is at best an *explanatory heuristic* in evolutionary explanations in which organismic activity and development can be "black-boxed" without losing explanatorily salient information, as for example in the case of the rise and decline of the melanistic morph in the peppered moth (*Biston* beularia) populations in industrial Britain. Thus, I take the niche construction perspective—that organisms can be active participants in evolution by manipulating selection pressures—as a given and refer the reader to chapter 3 and 4 for arguments in favor of that perspective. The target of this chapter is rather one *particular* theoretical and conceptual framework that grew out of the niche construction perspective—namely *niche construction theory*—which has become the canonical way to formalize and conceptualize the general view expressed by the niche construction perspective.

I will argue that the way niche construction is conceptualized on the version offered by niche construction theory (e.g., Laland et al. 2000; Odling-Smee et al. 2003) faces two problems:

(1) It excludes many ways in which organisms can actively modify their relationship with their environment. Importantly, the ways in which organisms can alter their own constitution (and consequently change the selection pressures acting on them) are not included.

(2) The standard niche construction categories are inconsistent with the standard understanding of a niche. That is, if a niche consists of the feature-factor relationships between organism and environment, and if niche construction is the modification of this relationship by the organism, then the standard niche construction categories (perturbative and relocational) are somewhat arbitrary and do not properly partition the possible forms of niche construction.

In light of this critique, I offer a reconceptualization that captures both the original sentiment of niche construction theory, but also makes room for forms of niche construction that fall outside of canonical niche construction theory but should nonetheless be considered niche construction.

Another aim of this chapter is to show that niche construction can be seen as a set of resources that supplement evolutionary theory. In so doing, I discuss the two main worries that skeptics have raised in relation to niche construction: its apparent ubiquity, and *how* it can play a role as an evolutionary cause or process. I argue that the reconceptualization of niche construction offered by this chapter can help us better understand niche construction's place in evolutionary theory by offering an account of how (i.e., what kinds of interactions) organisms can alter their selective environments and how those changes can be transmitted to succeeding generations for downstream effects (i.e., intergenerational mechanism of inheritance—that is, inheritance of organism constructed selection pressures).

Before offering the revised niche construction framework, I will describe in the following section how niche construction is standardly conceptualized on niche construction theory and point out some of the problematic aspects that follow from this conceptualization. I then offer an alternative framework and show how it improves on the standard account. Towards the end of the chapter, I will return to the question of how to understand niche construction in relation to evolutionary theory.

6.2 Niche Construction Theory

The main reference point for niche construction in the contemporary literature is the writings of Odling-Smee, Laland, and Feldman,[32] especially in their (2003) book *Niche Construction: The Neglected Process in Evolution.* In this chapter, it is the conceptual framework developed in this text that will mainly be discussed, however I will supplement with other texts when necessary. When I refer to 'niche construction theory' (or 'NCT') in what follows, it is to the conceptual framework of the Odling-Smee et al. (2003) and their more contemporary writings (e.g., Laland et al. 2016; 2019) which I refer.

6.2.1 The Standard Account of Niche Construction

For Odling-Smee et al. a niche is "the sum of all natural selection pressures to which [a] population is exposed" (Odling-Smee et al. 2003, 40). Defined as such, it corresponds to other selection-based conceptualizations of the environment, such as Brandon's (1990) definition of the selective environment discussed in chapter 2. The chief motivation behind this selection-based definition is to render the concept of niche—which is primarily understood in ecological terms—into a concept that can capture the evolutionary significance of niches. There are two other important points to note about the definition. First, it is relativistic: "the selection pressures are only the selection pressures relative to specific organisms [or specific traits of the organism]" (Odling-Smee et al. 2003, 40). Second, the niche has a dual nature: While it is common in ecology to define an ecological niche as either a portion of a habitat that can sustain a species (Hutchison 1957; Grinelli 1917) or as the role of an organism or species in its biotic environment (Elton 1927; MacArthur and Levins 1967), the concept of 'niche' in niche construction theory attempts to capture both of these aspects. That is, the niche is composed of the selection pressures that relate to the "lifestyle" or "occupation" (Ehrlich and Roughgarden 1987) of the organism and its habitat or "address" (Odum 1989). For ease of exposition, Odling-Smee et al. (2003) borrow

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[32] Many of these articles are referenced in this text, but for a full overview of the publications see: https://synergy.st-andrews.ac.uk/niche/our-publications/. The importance of niche construction has been argued for by others, see Brandon and Antonovics (1996); Oyama et al. (2001); Lewens (2003); Sterleny (2003); Boni and Feldman (2005); Donohue (2005); Chiu and Gilbert (2015); Sultan (2015).

terminology from Bock (1980), who proposed a scheme that decomposes an organism into different subsystems (traits and sets of traits) called ‘features’, and decomposes an organism’s environment into different subsystems (environmental variables) called ‘factors’. Selection pressures are then understood as factors selecting for features, and niche construction occurs:

> when an organism modifies the feature-factor relationship between itself and its environment by actively changing one or more of the factors in its environment, either by physically perturbing factors at its current location in space and time, or by relocating to a different space-time address, thereby exposing itself to different factors. (Odling-Smee et al. 2003, 41)

That is, niche construction happens when organisms are changing selection pressures through the modification of their physical environment or by changing habitats (Laland et al. 2016).

On NCT, an organism may alter the feature-factor relationship in several ways. For Odling-Smee et al. (2003), the primary ways in which organisms engage in such activities is through perturbative niche construction and relocational niche construction. The former describes cases where organisms change one or more factor in their physical environment, while the latter describes cases where organisms move and thereby expose themselves to different environmental factors. In any given episode, niche construction can, and in practice often will, be both perturbative and relocational.

Further, Odling-Smee et al. (2003) distinguish two contexts in which niche construction activity occurs: ‘inceptive’ and ‘counteractive’ niche construction. Inceptive niche construction occurs when the organism initiates a change in one or more of the factors in its environment, while counteractive niche construction involves counteracting change from the external environment. There are thus four categories of niche construction: inceptive perturbational, counteractive perturbational, inceptive relocational, and counteractive relocational.

Lastly, there is a difference between ‘positive’ and ‘negative’ niche construction. This distinguishes cases in which niche construction has beneficial (positive) or detrimental (negative) effects on the niche constructing organism’s fitness. The changes to selection pressures brought about by niche construction can be ephemeral or can persist for a long duration. Instances of positive niche construction is expected to spread throughout a population, given that the niche constructing traits have higher fitness values than alternative traits relative to a certain adaptive problem (Schulz 2014). The effects of niche construction can persist across generations through ecological inheritance. Simply put, it is not only the parental genes an organism inherits, but also the constructed environmental conditions into which it is born. Just as humans inherit (in a legal sense) money or land, so too can organisms inherit the ecological conditions of their parents or other conspecifics. However, niche constructing behavior can also persist through genetic inheritance. Nest-building birds and web-building spiders do not elaborate on previously built structures, nor do they take previous structures as templates for their creations, and in that sense do not enjoy ecological inheritance. However, they are still engaging in niche construction when they build a nest or web.

6.3 Two Problems with the Standard Account of Niche Construction

While the standard account of niche construction made progress on how to include the active role of the organism into evolutionary theory, I will argue that a reconceptualization is needed. I offer two key reasons for this. First, the categories of niche construction given by NCT do not map particularly well onto their conceptualization of the relativistic and interactive nature of an evolutionary *niche*. Second, their categories leave out of consideration organisms that can change their own phenotypic features and consequently alter the selection pressures acting on them. In the following two subsections, I will go through these two problems before offering an expanded conceptualization of the basic kinds of niche construction.

6.3.1 The Niche as a Result of Organism-Environment Interaction

As we have seen, niche construction theory is presented as an alternative to externalism. The niche is not a pre-existing physical space for the organisms to fit into, but rather composed of the interaction of traits (features) and environmental variables (factors) (cf. Lewontin 1983a, 2000, 2001; Odling-Smee et al. 2003). Niche construction occurs when an organism actively changes a factor—or its relationship with factors—in such a way that selection pressures are altered. In this way, organisms are active participants in constructing their adaptive fit, and consequently an explanation of this fit must refer to the activities of organisms that change the feature-factor relationship (in other words, the selective environment). Changes to the properties of the environment are thus not explained solely by other properties internal to the environment, but also by properties of the organism.

However, if a selection pressure results from the interaction of environmental factors and organismic features, and the niche is defined as the sum of selection pressures acting on a population (as it is in NCT), then organisms can actively change their niche by changing:

(1) Traits (features)
(2) Environmental variables (factors)
(3) The relation between the features and the factors.

The standard NCT conceptualization allows only for the modification of (2) and a limited set of (3) to count as niche construction. The part of (3) that is included is the modification of the relation between features and factors through relocation in space. However, it is arbitrary to leave out (1) and part of (3), and to do so is inconsistent with NCT's own definition of a niche. I therefore hold that niche construction should be reconceptualized to track all aspects of the niche that an organism is capable of modifying—that is, a modification of (1), (2), and (3). To further motivate the claim that niche construction should include modifications of (1) - (3), I will consider in the next subsection some cases of niche construction excluded from NCT, but which fit within an expanded account.

6.3.2 Organisms Changing their Own Features or Relations without Relocating

Organisms can modify the relationship between features and factors without needing to relocate or alter their features or the factors. For example, take meerkats (*Suricata suricatta*), which have constructed a very peculiar social niche. They have sentries, which are experienced meerkats that keep a lookout for predators while other members gather food. The division of labor and flow of information from sentries to other members of the group alters the epistemic environment of the group (Sterelny 2003; Dugatkin 1997). This is a case of 'social' (or 'epistemic') niche construction according to Sterelny (2003). However, it is unclear how this would be categorized using the standard categories of niche construction theory. While meerkats surely engage in perturbative niche construction through the creation of their burrows, the information flow through the sentries need not be perturbative or relocational. The meerkat sentry may encourage certain sorts of relocations not possible without it—allowing the other meerkats of its social group to gather food, play, and raise their young without constantly having to be on the lookout for predators—but the information flow itself does not seem to be a relocation as understood by the standard approach to niche construction.

Another example of niche construction falling outside of the NCT framework is how some organisms modify how they experience their environment (Chiu 2019; Chiu and Gilbert 2015; Sultan 2015). For example, an organism can modify how it experiences temperature through a behavioral, morphological, or physiological adjustment in which it modulates the thermal heterogeneity of its environment (Sultan 2015, 74-9). These are cases in which the organism need not change factors or relocate, but it nonetheless changes the relationship between the features and the factors such that the selection pressure is altered.

Following Walsh (2015), I label the kind of niche construction characterized by the active modifications of features 'constitutive niche construction'. Godfrey-Smith (1996) saw constitutive niche construction as a potential category of how organisms can be said to construct their environment (or niche) in his *Complexity and Function of Mind in Nature*:

> [A]nother sense in which organism can be said to construct their environment asserts not a causal, but a constitutive or ontological dependence. Features of the environment which were not physically put there by the organism are nonetheless dependent upon the organism's faculties for their existence, individual identity or structure. (Godfrey-Smith 1996, 145)[33]

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[33] It should be noted, however, that while Godfrey-Smith alludes to this as a possible way to understand how an organism can be said to construct its environment, he does not ultimately count it as organic construction: "Organic construction of the environment occurs whenever an organism intervenes in a formerly autonomous process in the physical world, changing their course and upshot". (Godfrey-Smith 1996, 145)

Godfrey-Smith points to what he takes to be a constitutive, and not causal, relationship. But I think that constitutive niche construction is causal, in that by changing its constitution, the organism changes the causal relations it has with its environment. Recent work (e.g., Sultan 2015; Walsh 2015; Chiu and Gilbert 2015) has embraced this mode of niche construction. These are cases in which there is a change in an organism's form or capacities (its features) and the factors of the environment that it experiences, without there being a change to the environment itself (Walsh 2015, 181-182).

A rich source of examples of this kind of niche construction can be found in the behavior of sessile organisms. Being limited by an anchoring point, sessile organisms cannot actively move in space, and are often limited to changing their constitution, primarily by the growth and discharging of body parts, in order to solve (or dissolve) certain adaptive problems, such as resource availability (Sultan 2015, 80-84). Arber (1950) made this point in connection to plant behavior:

> Among plants, form may be held to include something corresponding to behavior in the zoological field. The animal can do things without inducing any essential change in its bodily structure. When a bird uses its beak to pick up food, the beak remains unchanged. But for most, but not all, plants the only available forms of action are either growth or discarding of parts, both of which involve a change in the size and form of the organism. (Arber 1950, 3)

Growth and discarding of parts in plants often occur in relation to environmental cues, and the plants often do so in a flexible and adaptive way. Such plant behavior is usually conceived as instances of phenotypic plasticity (West-Eberhard 2003; Trewavas 2009; Sultan 2015). In relation to the standard approach of niche construction, much of the behavior in which sessile organism can play an active role in their own evolution therefore falls outside of the categories of niche construction theory.

In light of these problems, I offer a reconceptualization of the basic kinds of niche construction. In the following section, I provide a way of partitioning niche construction into three basic types: constitutive, relational, and external.

6.4 Three Kinds of Niche Construction

To clearly grasp the kinds of niche construction that exist and how best to categorize them, consider an FM radio and the ways that it could "construct its niche". When turned on, such a radio may receive a signal from a station and convert the electromagnetic waves into sound waves within the range of human hearing. Think of the sound output as the expression of the life of the radio. How does a radio construct its niche and what effect does it have on the outcomes of its life?

The example of the radio will help develop a tripartite distinction, to show that there are three fundamentally different forms of niche construction for biological entities.

6.4.1 Constitutive Niche Construction

The radio under consideration is constituted in a particular way, and its constitution influences the sound produced. The radio is engineered to receive radio waves in the FM frequency only. Electromagnetic signals outside of that range (AM radio signals, cell phone signals, and so on) are not received and do not affect the sound output—or if the output is affected, it manifests as an unwanted disturbance. The essential parts of the radio—the antenna, circuit board, speaker, power supply—constrain what is possible for the radio to output. There is a wide range of possible frequencies to which a radio can be tuned and the specific constitution of this radio narrows this down. The size and shape of the antenna constrains the space of possible frequencies that can be reliably received, and the electronics are tuned to be sensitive to a narrow band within this space. Furthermore, the acoustic equipment—such as the shape of the speaker and the nature of the amplifier—determine the possible range and characteristics of the sounds (volume, pitch, timbre, and so on). Thus, the very constitution of the radio (in part) determines its niche: its constitution carves out a slice of the world, making this and only this slice matter for the life of the radio.

But if the radio is not a mere passive subject, and is able to change its constitution, then it can construct its niche by changing itself. If it changes the size of its antenna or modifies its circuitry, then it could change its ability to receive signals and convert them into sound. Organisms are in this respect like radios. They are tuned to receive some aspects of the world, while being incapable of receiving others. For bees, ultraviolet light is visible, and this has a profound effect on how they perceive flowers. A dog can smell a deer that passed by hours ago, while we are incapable of detecting such diluted smells. Because organisms are dynamic entities, changing from moment to moment, they construct their niche through their behavior and development. A lion changes its size, strength, and coordination as it matures. Through this maturation, the space of possible prey is transformed. A lion in its prime may be able to take down a healthy mature wildebeest, but an immature lion will be restricted to the young, elderly, or diseased. The development of the lion is thus partly responsible for the construction of its niche.

This form of niche construction is not restricted to animals, and niche construction need not be linked to external movements. It is well known that plants respond to herbivores. For example, some plants will change their physiology in response to the vibrations caused by caterpillar chewing (Appel and Cocroft 2014). Such a physiological reaction is a form of constitutive niche construction. The plant increases its chemical defenses in response to the vibrations, thus changing its selection pressures.

6.4.2 Relational Niche Construction

Niches are carved out of the world via the constitutions of organisms, but they are also carved by the relations that the organisms bear to one another and to other factors of the biotic and abiotic environment. These relations can be modified in the absence of the organism transforming its own constitution or the physical conditions of its environment. This form of modification we label ‘relational niche construction’. Let’s return to the example of the radio to bring this into focus. Consider now a group of radios. These radios are passively receiving FM signals—their behavior in no way changes the output of the received signals. Nevertheless, the radios can influence one another’s life. For example, if one radio is standing before another one, the characteristics of the received signal will be modified, however slightly. If the radios touch their antennae together, the signal reception will change more significantly.

If the radios were equipped with wheels and navigational equipment, they could increase their proximity to the source of the radio signal. This would provide a stronger, clearer signal, though it will not change the source of the signal (and is thus still passive with respect to the signal).

Organisms, especially social organisms, can construct their own niches via relational niche construction. Mice that pile up to keep warm are not keeping warm by changing the temperature of their nest. But they can affect their own rate of heat loss—and the heat loss of their nest mates—just by existing in a particular proximity to others. Alpha males and females in social primate species have significant effects on the behavior and physiology (stress levels, for instance) of others in the group merely by being present. Their presence may also alter the access to food sources of other members of the group. These alterations are not due to the alphas altering the physical environment but are instead based on the relation between the alphas and the other members of the group.

A niche is filled with information that organisms can use to solve adaptive problems. For example, some prey prefer to be in a close proximity to their predators, because if they are constantly receiving information about the location of the predator, then they are less susceptible to fatal surprise encounters (Sterelny 2003). In such cases, prey often move in space to keep a steady stream of information about the location of the predator flowing. Such relocational niche construction is best understood in terms of information flow and its consequences. They relocate not to change the world or themselves, but to keep certain channels of information open.

Relational niche construction can also involve relocation for food or mates or nesting sites or any other selection-relevant resource. A deer that moves up the mountain in the summer to dine on rich alpine grass is, via its movement alone, relationally constructing its niche. But the deer is apt to also be actively changing the external environment during its migration. It might, for example, be helping to maintain a system of trails. Let’s now consider the idea of constructing the external environment, and how this differs from relational construction.

6.4.3 External Niche Construction

Niche construction can involve the modification of the environment, changing not merely the form of interaction with environmental factors, but the very factors themselves. If the radio were able not just to react to the available stations, but to modify them or to create its own, it would be engaging in ‘external niche construction’. A group of radios that set up a pirate radio station would be changing the external FM band environment.

The prototypical example of external construction in organisms is beavers building dams (Jones et al. 1994, 1997). Beavers cut down trees to dam rivers. The dams block the passage of water, creating a pond. The beavers then travel around by swimming in the water. The constructed pond exerts selection pressures, selecting for water-related traits like a waterproof coat and webbed feet.

External niche construction is not limited to the modifications of an organism's and its conspecific's own selection pressures, however. Just as the beavers modify their own selection pressures by building a dam, they are modifying the selection pressures of all the fauna and flora in that immediate area. They are creating an environment for aquatic organisms (within the pond) and are making a large area for moisture-loving plants (willow trees, for example) around the pond.

6.5 Conceptual Improvement on Niche Construction Theory

In the preceding section, I've characterized three kinds of niche construction: constitutive, relational, and external. How does this characterization differ from—and why might it be an improvement over—the standard account from niche construction theory? In this section, I discuss how the tripartite characterization improves on the standard categorization.

Constitutive Niche Construction: Constitutive niche construction is left out of consideration on the standard account of NCT. The significance for ecology and evolution of the constitution of organisms is by no means overlooked by proponents of NCT (Laland et al. 2014b). However, they standardly exclude changes in constitution from niche construction. Above I argued that this was a problem for NCT, now I will provide some further argumentation in favor taking constitutive niche construction into consideration.

If an organism's niche is defined by the feature-factor relationship between itself and its environment, then a modification of the feature-factor relationship will be an instance of niche construction. As we saw above, there are three ways that the feature-factor relationship can be modified, the first of which involves a change in the features. Thus, if a niche is defined in terms of a feature-factor relationship, and if niche construction is the modification of this relationship, then actively changing the features should be classified as niche construction.

Additionally, many changes to an organism's constitution cannot fully be explained without a reference to the effects (or adaptive consequences) its altered constitution has on the organism-environment interaction. For example, in the case of drought a plant might droop or roll its leaves during the day when the plant experiences the highest rates of transpiration, the phenomenon called wilting (Begg 1980). At night, with a decline in transpiration, the rolled leaves slowly re-expand (Fang and Xiong 2015). Cases of constitutive niche construction are not limited to plants and other sessile organisms. Humans, too, can change their constitution. For example, the plastic physiological response involved in muscle growth is influenced by how humans engage with certain environmental factors (Gilbert and Epel 2015).

Relational Niche Construction: Relational niche construction is a more expansive concept than NCT's *relocational* niche construction. Relocational niche construction occurs when organisms alter their spatiotemporal relationship with the external environment. However, organisms can also alter their relationship with other organisms, both conspecifics and heterospecifics. And such alterations do not necessarily involve changes in location. The important changes are those of relationships, not locations. Thus, relational niche construction captures organismic alteration of spatiotemporal relationships to the environment, as well as the alteration of the relationships it has with other organisms.

Habitat selection—the process by which organisms choose areas of their environment where they conduct specific activities (Stamps 2009)—and migration are examples of relocational niche construction. In such cases it is clear that an organism alters its spatiotemporal relation to the external environment and thereby alters its selection pressures. However, a vast array of complex social and inter-organismic behavior, such as the meerkats' 'social security' niche, social hierarchies in primates, and human domestication of animals and plants[34] consist in a large degree of the alteration of organism-to-organism relationships, and not only the alteration of the organism's spatiotemporal relation to the external environment.

Thus, the NCT concept of relocational niche construction is too narrow. Relocational niche construction is not a basic form of niche construction but is instead one way of achieving relational niche construction. It is the relations that are

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[34] See Zeder (2016) for a treatment of domestication from a niche construction perspective.

fundamental, and while relocating can change relationships, it is not the only way to do so. The gaps in relocational niche construction are particularly apparent when attempting to categorize niche construction via transformations in the flow of information, as in epistemic and social niche construction (Sterelny 2003).

External Niche Construction: While the category of external niche construction might be more of a label change than a conceptual innovation, it seems more appropriate to use 'external' as the label, instead of the NCT's 'perturbative'. These cases are, according to NCT, niche construction activities where there is alteration of the external (or physical) environment. But the concept of perturbation does not by itself distinguish between, for example, the perturbation of physical and social environments. A lone adult lion might challenge an older and weaker male lion for control of its pride and usurp its place as leader of the pride. This is a perturbation of the social structure of the pride but is not an alteration of the external (or physical) environment as conceived by NCT. It would be a case of relational niche construction. Additionally, an organism can perturb itself: for example, it could estivate or hibernate, in which it reduces its metabolic activity and rests for a long period. Such self-directed perturbation would be classified as constitutive niche construction. Perturbation refers to a kind of action, while external refers to what is involved in the action. As such, external niche construction offers a more precise way to pick out and classify niche construction activities involving changes to the external environment.

6.6 The Status of Niche Construction Theory Within Evolutionary Theory

Much of the contemporary literature on niche construction centers on the utility of the niche construction framework. There are several areas in which a niche construction perspective appears to clarify or to advance other related topics in research on culture, archaeology, primatology, and much more (see Laland and Sterelny 2006). Other literature, however, directly addresses and critiques niche construction theory. These critiques have been general and focus primarily on how niche construction relates to evolutionary theory. As such, these are worries that any concept of niche construction must deal with. Before I respond to offer to these worries, let me briefly summarize what I take to be the most important criticisms levelled against niche construction.

There are two main lines of critique against niche construction. One concerns the helpfulness of adding niche construction to evolutionary theory, while the other concerns whether niche construction should be understood as a true evolutionary process on par with selection. The arguments against the helpfulness to evolutionary theory hold that the niche construction framework does not improve on the already existing framework of the modern synthesis. Problems such as the intractability, a lack of predictability, and the ubiquity of niche construction are their main worries (Brodie 2005; Dawkins 2004; Griffiths 2005; Laland and Sterelny 2006; Okasha 2005; Sterelny 2001, 2005). The arguments over the status of niche construction as a process concern, as we saw in chapter 3 and 4, skepticism about whether niche construction is, or should be, viewed as a process in addition to standard evolutionary processes such as selection and drift (e.g., Scott-Phillips et al. 2014).

6.6.1 Is Niche Construction a Helpful Addition to Evolutionary Theory?

One argument against the theoretical value of niche construction is that of Dawkins (2004), who argues that it might be better regarded as a background condition than as causal difference maker. The justification given for this is that since evolving systems are so complex, we cannot study them without making simplifying assumptions. Incorporating the feedback—or reciprocal causation—generated by niche construction could very well mean one complication too many. Further, there might be cases in which the apparent niche constructive activity was selected by prior natural selection. As such, the activity that changes selection pressures is a result of natural selection and the explanation of it does not need to be any more complicated (in terms of causal complexity) than what is already available in the standard picture (cf. the extended phenotype, Dawkins 1982). This is thus an argument that while there is niche construction, it may be best to leave it out of evolutionary models, as including it might not even alter the resulting evolutionary dynamics enough to warrant the increased complexity.

There is also the argument that niche construction is so ubiquitous that it should not be identified as a separate phenomenon. The worry about the ubiquity of niche construction stems from the (intentionally) broad definition of niche construction (Laland et al. 2016). All organisms can potentially be considered niche constructors, since the definition requires only that an organism alters selection pressures through environmental modification. Including constitutive niche construction within the scope niche construction appears to make this even worse, as this renders any biotic change into a potential case of niche construction. There might be severe consequences of having such a ubiquitous concept at play. First, it appears to render niche construction intractable. Since every selection-relevant interaction counts as niche construction, and since we obviously cannot factor in every interaction into our models, how are we to know what are the important cases of niche construction? Second, the ubiquity of niche construction also seems to marginalize its potency as a causal difference maker in evolution, thus challenging its explanatory significance. Unless we have some sort of demarcation principle between significant and insignificant cases of niche construction, what role can invoking niche construction play in explaining adaptation? What seems to be needed is a way to distinguish significant and insignificant (Matthews et al. 2014) and/or adaptive and accidental (Sterelny 2005) cases of niche construction, and a way to narrow down the set of behaviors that fall under the rubric of niche construction.

My response to these worries is that the ubiquity of niche construction is no reason to hold that niche construction is trivial or lacks explanatory relevance, and that the idea that niche construction is a mere background condition is not supported by the importance of niche construction in many evolutionary systems. Consider two central ingredients of evolutionary explanations, selection and drift. Both are ubiquitous. Populations are subject to a multitude of selection pressures. Some of these pressures are so weak that they can be ignored, while others are powerful and can serve in explanations of evolutionary outcomes. Pointing out that selection pressures are ubiquitous does not decrease their importance, much less render them trivial. Thus, just as there are strong selection pressures that we should foreground in our analysis of evolutionary events, while we can safely ignore others, so it is with niche construction. Constructing models always involves simplification and the backgrounding of some factors while foregrounding others. That fact that there will be many forms of niche construction in the background does not mean that all should be relegated to the background.

Drift is also ubiquitous (e.g., Ramsey 2013c), and its evolutionary effect approaches zero as the population size tends toward infinity. Thus, in large populations, especially over short time scales, we could leave drift out of our models. But the ubiquity and at times irrelevance of drift does not mean that it is unimportant.

Drift is crucial in understanding the dynamics of small populations, and the ubiquitous drifting of noncoding genes can provide information about such things as divergence times in lineages (e.g., Rannala and Yang 2007).

Drift and selection are thus ubiquitous, but in any evolutionary system, not all drift and selection pressures are equally important. Additionally, we often want to understand the extent to which drift and selection played a role in particular evolutionary events. If we observe that an island population of monkeys has lighter fur than the nearby mainland conspecifics, we can ask if this is an evolutionary response to selection, or if it is drift, or both. Similarly, what is important with niche construction is not whether constitutive, relational, or external niche construction are at play in an evolutionary system, but the relative significance of each in accounting for a particular evolutionary outcome.

Like with drift, selection and other evolutionary factors, ubiquity does not imply triviality, nor does the fact that niche construction explanations are not always necessary imply that they are never important.

6.6.2 Is Niche Construction an Evolutionary Process?

As we have seen in chapter 3 and 4, there is an ongoing debate concerning whether niche construction is a process on par with natural selection (Laland 2015; Scott-Phillips 2014). While some advocates of the niche construction perspective argue that niche construction is an evolutionary process in its own right—one that biases the action of natural selection by either directing or counteracting its effects (Laland 2015, Laland et al. 2017), critics have responded by arguing that there are only four 'proper' evolutionary processes: mutation, recombination, natural selection, and drift. The first two are processes that generate phenotypic variation, while the latter two are processes that sort that variation. Niche construction, according to these critics, is one of many factors that can influence either of these processes (Scott-Phillips et al. 2014).

I have already argued why I think conceiving of niche construction as an evolutionary process on par with natural selection is problematic—as it inadvertently renders natural selection a purely environmental process, which it is not. So instead of rehearsing those argument here, let my rather show *how* niche construction can be integrated into evolutionary theory as a theoretical framework designed to allow organismic activity and development to figure in explanations of evolutionary events.

An organism's active modification of its selective environment can be decomposed into an array of different mechanisms. By showing how mechanisms acting within an organism's lifetime (intragenerational) are related with mechanisms acting across generations (intragenerational), we can see how organismic activity can facilitate an evolutionary response (in other words, to show how ontogenetic and behavioral mechanisms can have evolutionary effects). In table 6.1 I show how the tripartite conceptualization of niche construction helps us understand the diverse way in which organisms can engage in niche construction, and the diverse mechanisms that can facilitate an evolutionary response to the niche constructing activity.

	Constitutive	**Relational**	**External**
Intragenerational Mechanisms	Phenotypic plasticity, behavioral innovation.	Behavioral plasticity (without alteration of the external environment), relocation, resource management, social learning.	Ecological engineering; for example, web or nest building. External alterations during an organism's life-history.
Intergenerational Mechanisms	Parental effects (prenatal), epigenetic inheritance, genetic inheritance.	Behavioral/social and cultural inheritance, parental effects (postnatal).	Ecological inheritance.

Table 6.1. Top row: Mechanisms acting within generations that can alter selection pressures. Bottom row: Mechanisms that reach across generations in modifying selection pressures. The list is meant to be illustrative and not exhaustive.

Table 6.1 is meant to do two things. First, it helps to make niche construction more tractable, pointing out mechanisms through which organisms may alter their selection pressures. Second, it highlights the diversity of these mechanisms, and shows that in specific evolutionary systems, and for specific evolutionary questions, we can safely background some of these mechanisms while foregrounding others. A species may be behaviorally plastic without being innovative (Ramsey, Bastian, and van Schaik 2007), and even if it is innovative, we might be able to leave innovations out of the model for our study at hand. Similarly, a species might be innovative without being cultural (Jablonka and Lamb 2014; Ramsey 2013d), but even if it is cultural, the culture may not be significant for understanding a particular evolutionary outcome.

Thus, I think niche construction theory should be seen as a phenomenon that captures a wide set of mechanisms that yield novel explanatory and theoretical resources for investigating the active role of organisms in their own evolution. Apprehending the interplay of these mechanisms can result in a more detailed and nuanced understanding of evolutionary dynamics. The conceptualization of niche construction offered here, coupled ecological and interactionist approach to natural selection defended in the preceding chapters, allows for niche construction theory to be an integrated part of standard evolutionary theory picking out the different means by which organisms can actively produce and maintain adaptive responses through the manipulation of selective environments.

6.7 Conclusion

In this chapter I offered a reconceptualization of niche construction. I argued that the traditional conceptualization of the basic kinds of niche construction offered by niche construction theory faces two problems. First, if a niche is constituted out of the feature-factor relationship, the basic kinds of niche construction should map onto such an understanding of a niche, and any modification of this relationship should therefore count as niche construction. These modifications can be changes in features, in factors, or in the feature-factor relationship. Second, there is a whole class of cases that are left out of consideration by the standard conceptualization of niche construction. Importantly, organisms can alter their own features, thereby altering their selective environment. To address these problems, I offered an alternative account and identified three corresponding forms of niche construction: constitutive, relational, and external construction. This is an expansion and reworking of the traditional account, which includes only two forms of niche construction, perturbative and relocational.

I then showed how the tripartite reconceptualization can help make progress in two common debates in the contemporary literature on niche construction: Its causal role in evolutionary theory and the question of whether it is a helpful addition to evolutionary theory. For the latter, I showed how both natural selection and drift are ubiquitous, but that this does not undermine their role in understanding evolutionary dynamics. Similarly, with niche construction, the fact that it is ubiquitous does not undermine its potential for increasing our understanding of evolutionary systems.

On the question of niche construction as an evolutionary cause, I used the tripartite conceptualization to show how the three different types of niche construction activities can be divided into two sets of mechanisms—intragenerational mechanisms and intergenerational mechanism—both of which allow niche construction to have evolutionary effects. I then argued that by isolating the mechanisms responsible for an occurrence of niche construction, it will help clarify when the niche construction perspective is appropriate and useful. In the next chapter we shall look move from the causal-mechanistic structure of niche construction to its *teleological* structure. Organisms are goal-directed creatures, which means that niche construction itself—being fundamentally an organismic activity—can be goal-directed.

7

NICHE CONSTRUCTION AND TELEOLOGY

7.1 Introduction

Niche construction, as have seen, refers to cases whereby organisms, through their activities—from metabolism to behavioral choices—alter environmental conditions and consequently engender changes to selection pressures acting on natural populations (Odling-Smee 1988; Odling-Smee et al., 2003; Laland et al. 2000, 2016). This construal is intentionally broad and essentially labels *all* organisms as niche constructors (Laland et al. 2016). In fact, this is what niche construction theory refers to as *obligate niche construction* (Odling-Smee et al. 2003). Obligate niche construction is simply a necessary feature of life, as living organisms are open systems in a far from equilibrium state and need to extract energy from their surroundings in order to maintain their internal order and dynamic stability (Schrödinger 1944; Odling-Smee et al. 2003, 167-79). The idea behind obligate niche construction was central to early 1900s organism-centered approaches to biology, and niche construction theory can thus be seen, at least on this point, as continuing in these traditions' footsteps (Baedke 2019; Nicholson 2018).

However, even in death organisms can still contribute as niche constructors. In what is called *ghost niche construction*, a decomposing carcass is altering the selection pressures of nearby scavengers, detritivores, and a host of microbial organisms (Odling-Smee et al. 2003). Obligate and ghost niche construction thus make niche construction a ubiquitous phenomenon and a process which does not require behaviorally complex organism-environment interactions. Sometimes, the way in which an organism subsists can create opportunities for alternative subsistence strategies for other organisms. The oxygenation of earth, initiated by cyanobacteria around 3,6 billion years ago, is an example of this (Laland et al. 2014c; Stal 2000). Their autotrophic lifestyles opened the possibility for heterotrophic lifestyles (as well as aerobic bioenergetic strategies in general). Niche construction of this kind—in which organisms open new niches for other organisms through their byproducts—is now well established (San Roman and Wagner 2018). There are also cases of facultative niche construction, such as beavers building dams with internal lodges (Jones et al. 1994, 1997), primates playing complex social roles and exhibiting (pre)cultural traditions (Flack et al. 2006), and lastly, humans, whose niche construction is unparalleled in terms of ecological consequences and behavioral complexity (Fuentes 2017; Sterelny 2003). Niche construction thus occurs along a continuum of organismic activity, from simple metabolic activity to complex behaviors.[35] But does 'niche construction' refer to the same thing in these different instances?

In this chapter I will argue that we should distinguish between two ways organisms in which organisms engage in niche construction: through purposive alteration to the environment and through non-purposive alteration. Both kinds of niche construction might constitute relatively simple organismic activity or be instances of complex behavior.[36] However, these two ways reflect two different *roles* organisms can play as active participants in development, ecology, and evolution; either as *agents* or as *contributors*. In cases of niche construction where the organism

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[35] In extreme cases it could even occur passively, like *ghost* niche construction mentioned above.

[36] In the rest of the chapter, I will frequently use the distinction between goal-directed vs. non-goal-directed 'behavior' to flesh out the difference between agential and contributional niche construction. This is merely terminological shorthand for "goal-directed vs. non-goal-directed organismic activity and behavior". Another terminological decision worth noting is that I take 'purposive' to mean the same thing as 'goal-directed'.

is regarded as an agent, an account of *why* the niche construction occurs requires a teleological explanation to fully account for the niche constructing behavior. When organisms are regarded as contributors, a teleological explanation of why the niche construction occurs does not have any bearing on the organisms' role as *contributors*. The distinction is important because asking whether an instance of niche construction is agential or contributional (or both) can potentially uncover novel explainable regularities that might otherwise remain unidentified. Further, interpreting niche constructing behavior as *agential* allow us to use niche construction theory to highlight important instances in which organisms across the tree of life exhibit *agency* and how instances of agency might have profound influences on developmental and evolutionary processes.

7.2 Different Definitions and Conceptions of Niche Construction

The literature offers a variety of different definitions and conceptions of niche construction, the broadest one being *obligate niche construction*. As we saw above, on this conception, niche construction is simply something that organisms must engage in to be alive (Odling-Smee et al. 2003). This conception has been criticized for its breadth (e.g., Brodie 2005; Okasha 2005), as it classifies all organismic activity as niche construction. These criticisms often amount to worries about empirical intractability and triviality due to being ubiquitous (e.g., Dawkins 2004). However, ubiquity alone is weak criticism. As I argued in chapter 6, and as Aaby and Ramsey (2019) argue, other evolutionary processes like natural selection or random genetic drift are equally ubiquitous. However, this does not mean that these concepts refer to trivial or intractable biological processes. It just means that there are cases in which the effects of the processes are more or less significant. For example, the effects of drift are inversely proportional to population size. As the population size increases, the effects of drift decrease. Similarly, the strength of positive selection is relative to how advantageous the phenotype under selection is relative to other phenotypes in the population. In a large population, or one with few extreme phenotypes, the effects of random genetic drift and (directional) selection may be negligible. But this does not mean that they are trivial *processes*. It just means that there are instances in which the effects are significant, but also instances in which they are negligible.

When the effects of a process are negligible, we usually background the process when we study the dynamics of the system, however if they are significant, we foreground them. Similarly, niche construction is a process that is ubiquitous, and when it has small effects, we can background it. At other times, it is exactly the effects of niche construction we want to study. This is reflected in Laland et al.'s (2016) definition of niche construction as "the modification of selective environments by organisms" (191). While still broad, this definition picks out what *kinds* of organism-induced changes are important—namely those that engender an alteration of selective environments. However, this definition is not without qualification. Laland et al. (2016) point to three criteria suggested by Matthews et al. (2014, 247) to operationalize the definition. These are: (i) the environmental modification must be *significant*, (ii) the effects of the niche construction activities must alter the selection pressures of some recipient organisms, and/or (iii) there must be a detectable evolutionary response to the altered environmental states brought about by the niche construction activities. The first two criteria are meant to capture all cases where the organism-mediated environmental modifications are instances of niche construction, while the third criterion is meant to capture the cases where evolutionary trajectories are influenced by organism-mediated changes to selection through environmental modification.

While this conception is still broad and captures a vast array of organism-environment interactions as niche construction, this is, as Laland et al. (2019) argue, intentional:

> The breadth of our definition reflected the job we wanted the term to do. We wanted to draw scientific attention to the diverse ways in which organisms modify environmental states, and the myriad of important ecological and evolutionary consequences that follow from these activities. (Laland et al. 2019, 130)

A broad conception of niche construction thus serves to capture the many diverse ways in which organisms can actively participate in their ecology, development, and evolution. 'Niche construction' could thus be considered a bucket term, and to understand how, when, and why niche construction is important, we should distinguish among specific kinds of niche construction.

7.3 Specific Forms of Niche Construction

We already considered *obligate* and *ghost* niche construction from Odling-Smee et al. (2003). However, their book contains several other more specific forms of niche construction. I discussed some these in chapter 6, but I will briefly address them here as well. First, Odling-Smee et al. (2003) distinguish two ways in which organisms engage in niche construction: through *perturbation* and *relocation*. Perturbational niche construction occurs when organisms change the physical environment, while relocational niche construction occurs when organisms move in space and time and consequently expose themselves to different environmental variables.

Odling-Smee et al. (2003) also make a distinction between two contexts in which niche construction can occur: *inceptive* and *counteractive*. Inceptive niche construction occurs when it is the organism itself that initiates the niche construction activity, while counteractive niche construction occurs when an organism counteracts changes in the environment. These can be combined to give us four categories of niche construction: inceptive perturbational, counteractive perturbational, inceptive relocational, and counteractive relocational. These four categories can further be categorized as *positive*, *negative*, or *neutral*, depending on their effects on the niche constructing organism's fitness. Finally, Odling-Smee et al. (2003) also identify *cultural* niche construction. This refers to the effects cultural traits can have on other biological or cultural traits, and on other species (Fogarty and Creanza 2017; Laland and O'Brien 2012).

Sterelny (2003; 2010) uses the concept of niche construction to argue that a crucial part of the story of human cognitive evolution is our ability to construct social niches and modify our epistemic environment. *Social* niche construction consists in the modification of relationships between conspecifics, which consequently alter selection pressures. An example of this is the different social roles of adult meerkats (*Suricata suricatta*) in their troops. *Epistemic* niche construction consists in altering the information flow from the environment, without necessarily altering the environment itself. Predator-inspection strategies—when prey move closer to be able to locate and track potential predators—is an example of this.

Another form of niche construction is *experiential* or *mediational* niche construction (Sultan 2015; Chiu 2019). For Sultan (2015) there are two types of niche construction: habitat construction and experiential construction. Habitat construction occurs when the physical environment is altered (similar to perturbational niche construction above). Experiential (or mediational) niche construction occurs when an organism modifies its experienced environment without altering the physical environment. The experienced environment of an organism is a combination of environmental cues and the response to such cues. The cue is a placeholder, and what counts as a cue is relative to the organism's specific sensory system and transduction pathways, as well the environmental factors it engages with. Habitat choice thus counts as an example of *experiential* niche construction.

Organisms also change the way they experience their environment by changing their own constitution. Many plants change the morphology of their leaves depending on light conditions. In low-light conditions, leaves become larger in surface area to capture more photons. In high-light conditions it is beneficial to have smaller but more numerous leaves, since too much exposure to ultra-violet light can damage plant tissue (Sultan 2015). Thus, by altering their leaf morphology, plants modify their experienced environment. This kind of niche construction, through an alteration of the organism itself, has been called *constitutive* niche construction by others (Aaby and Ramsey 2019; Walsh 2015; see also chapter 6).

The final kind of niche construction I will discuss is Ikiri and Sakura's (2008) *intentional* niche construction. This refers to an organism's capacity to deliberately (in terms of higher-order intentional states, e.g., planning) manipulate their environment. Ikiri and Sakura (2008) argue that tool-use and tool-manipulation together with ecological and (proto)cultural inheritance and *passive* niche construction (i.e., non-directed environmental modification by organisms) allowed the hominid linage to increasingly exploit the capacity for intentional niche construction. They argue that the rapid encephalization experienced by the hominid linages over the last 2 million year, which led to incredible diversity of cognitive capacities we see in the hominids post *Homo habilis*, was in part due to an increasing capacity of intentional niche construction. The capacity of intentional niche construction changed the selective environment these hominids experienced into one that was predominantly determined by cognitive capacities. This in turn would have a ratcheting-effect on subsequent adaptation, leading to the rapid encephalization seen in the later hominids.

While this is not an exhaustive discussion of different ways the concept of niche construction has been utilized in the literature, it shows the extent to which the concept has been adopted in different contexts. In chapter 6, I showed how all such specified instances of niche construction can be subsumed by three fundamental categories of niche construction: *constitutive*, *relational*, and *external*. The reasoning behind this tripartite categorization is that since a niche is defined as the functional relationship between an organism and its environment, niche *construction* is any alteration of this relationship. Thus, niche construction can involve a modification to the organism itself, the environment, or the relations between the organism and its environment. The thought, then, is that since these categories track all the manipulable parts of the niche itself, it will cover all *specified* instances of niche construction. Further, I also made a distinction between intra- and intergenerational mechanisms. All three manipulable dimensions of the niche have important mechanisms associated with them, both during development and across generations. For example, an important intragenerational mechanism in constitutive niche construction is phenotypic plasticity, while an important intergenerational mechanism is epigenetic inheritance. For relational niche construction, behavioral plasticity is an important intragenerational mechanism, while social learning is an important intergenerational mechanism. While all instances of niche construction can be captured by the tripartite categorization, it is not sensitive to whether or not the niche construction is a goal-directed process. This is primarily because the tripartite categorization aimed to capture the causal-mechanistic structure of niche construction theory. However, as I argue below, there is an additional *teleological* dimension to niche construction not captured by the tripartite categorization—namely whether or not the niche constructing effects are a product of goal-directed behavior.[37]

7.4 Niche Construction and Teleology

In order to properly appreciate the difference between cases of niche construction that are goal-directed and those that are not, I want to draw on two examples in which the concept of niche construction is used to account for the relevant phenomenon—in bacterial cross-feeding and in the case of developmental plasticity in leaf morphology.

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[37] This distinction has been gestured at by Sterleny (2005) with his distinction between designed/adaptive and accidental niche construction. Brodie (2005) and Dawkins (2004) made similar distinctions as well. Such a distinction is problematic, however, as there are instances of accidental niche construction which are also adaptive. See Kylafis and Loreau (2008).

7.4.1 Niche Construction in Cross-Feeding Bacteria

In a paper on bacterial niche construction, San Roman and Wager (2018) showed the immense potential for niche construction in cross-feeding bacterial strains. Cross-feeding refers to an interaction in which one organism depends on the organic products of another organism for its subsistence. In the case of bacteria, cross-feeding often happens when mutant strains are able to metabolize the excrement of a different strain. For example, in evolutionary experiments on genetically identical *Escherichia coli* populations grown in homogenous environments where the only carbon source is glucose, it is common to see cross-feeding *E. coli* strains emerge. One way this can occur is when some *E. coli* cells that consume a primary carbon source (e.g., glucose) excrete a secondary carbon source (e.g., acetate). After some time, a polymorphic *E. coli* cell turns out to be able to metabolize acetate and consequently, usually through horizontal gene transfer, a strain of cross-feeding *E. coli* is established. Thus, in the case of cross-feeding bacteria, new niches are constructed solely out of the excretions of other organisms.

7.4.2 Niche Construction Through Alteration of Leaf Morphology

An important instance of developmental plasticity in plants concern the production of different leaves by the same genetic individual under different light conditions (Sultan 2010, 2015). Under low light conditions, a plant will produce thin, wide "shade-leaves." Under high light conditions, the same individual will produce thick, narrow "sun-leaves." Depending on the cues from the environment, in this case the density of photons, the plant will alter its constitution such that its experienced environment becomes different. Thus, the production of shade-leaves will transform the experienced environment from one with a lower to one with a higher photon density. Sultan (2015) interprets this as experiential niche construction (or 'mediational' niche construction *sensu* Chiu 2019):

> An equally universal aspect of niche construction [obligate niche construction being the other] 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 external parameters. (Sultan 2015, 41)

Seeing that an environment is not restricted to physical features external to the organism, but also includes how it is experienced by the organism, it seems reasonable that an alteration of how an organism experiences the environment can be understood as niche construction. In this case, the causal basis of the niche construction activity is an alteration to the plant's constitution, which has the effect of modifying the experienced environment without altering the physical environment. In the conceptual landscape outlined in section 7.3 and in chapter 6, this would be experiential/mediational *and* constitutive niche construction.

7.5 Explaining How and Explaining Why

In providing an explanation of *how* both the cross-feeding bacteria and leaf-altering plants are engaged in niche construction, standard causal-mechanistic explanations are readily available. In the case of the bacteria, the explanation might cite mechanisms responsible for the metabolism of glucose and acetate consuming *E. coli* cells, as well as the mechanisms of horizontal gene transfer. In the case of the production of shade-leaves, an explanation might cite biomass allocation and other mechanisms responsible for developmentally plastic responses in the plant.

An explanation of *why*, on the other hand, would not share an explanatory structure. In the case of the bacteria, an explanation of why it emits energy rich metabolites would be extremely general, probably citing the necessity of organisms to emit waste products when metabolizing. In the case of the plant, however, an explanation of *why* the plant produces shade-leaves would provide the *purpose* which that particular behavior serves in relation to attaining a specific *goal*.[38] The plant produces shade-leaves *in order to* increase light capture. This again can be explained in terms of biological function, i.e., the adaptive benefit higher light capture affords the plant. Thus, the difference between the case of the cross-feeding bacteria and the leaf-altering plant is that the latter needs a teleological explanation as well as a standard causal-mechanistic explanation to properly explain the niche constructing behavior. In the former, an answer to the *how*-question is sufficient explain how acetate excreting

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[38] I consider something like the production of leaves in plants *behavior* as it is something that the plant *does* and not something that *happens* to it, see Dretske (1988) for this approach to the concept of behavior.

bacteria engage in niche construction.[39] Why do *E. coli* bacteria excrete energy-rich metabolites such as acetate? Because that is the waste product of their bioenergetic strategy. The answer has no bearing on whether there are, or can be, cross-feeding strains that consume it.

We are now in a position to make a distinction between cases in which the niche constructing effects are goal-directed and not. A capacity for goal-directed behavior is often linked to agency. For example, Walsh (2015) argues that agency consists in:

> [A] capacity of [a] system to pursue goals, to respond to the conditions of its environment and its internal constitution in ways that promote the attainment and maintenance of its goal states. […] Agency consists in the capacity of a system to cope with its setting, to attain its goal by responding to its affordances *as* affordances. (Walsh 2015, 210)

On Walsh's view, agency is found within an interdefinable triad of concepts: *goals*, *affordances*, and *repertoire*. A goal is the end-state to which the behaviors or activities of a system are directed. An affordance consists in the conditions that are experienced by the goal-directed system as opportunities or impediments to the attainment of a goal. Finally, a repertoire consists of the set of capacities available to the system in pursuing its goal. A benefit of understanding agency as a capacity located within this triad is that it allows agency to come in degrees. A repertoire with a large set of behavioral capacities will increase the number of affordances, which further increase the flexibility and freedom of the system in pursuing its goal. We shall return to the relationship between teleology and agency in more detail in section 7.7.3 and in 8.3. For now, I suggest that niche construction behaviors that are goal-directed, or susceptible to teleological explanation, should be labeled *agential niche construction* because of the link between goal-directed behavior and organismic agency.

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[39] A clarificatory comment might be useful here. When I talk about cases of niche construction that are a product of goal-directed behavior, I mean that the consequences of the niche constructing behavior is the goal of the behavior that produces it. Thus, niche construction that is not the product of goal-directed behavior can still be a consequence of behavior that is *directed* at something else. The cross-feeding bacteria example shows this, metabolism is clearly a goal-directed process, but the goal of the process is *not* to excrete energy rich metabolites.

In cases of niche construction that are not goal-directed—such as the cross-feeding bacteria—the organisms are still *actively* engaged in niche construction. The niche constructing effects are still a result of what organisms *do* (perhaps excluding the case of *ghost* niche construction). The important aspects of these instances are not what the niche constructing behavior is directed at, but rather who and what are affected by it. In other words, what the niche constructing behaviors *contribute* to. Sometimes the contributions are global and stable across evolutionary time, and even necessary for the viability of a large chunk of the tree of life—as in the case of photosynthesis. Other times the contributions can be more local. The important aspect of these cases is their contribution to ecology, development, and evolution, which is why I label such instances *contributional* niche construction. We are thus left with two different ways in which organisms can be active participants in ecology, development, and evolution through niche construction: as *agents* and as *contributors*.

7.6 Why are Non-Reductive Teleological Explanations Important?

Now that we established that there are two different ways in which organisms can be active participants—as *agents* and as *contributors*—we need to show that this distinction plays a significant role for our understanding of niche construction and the active role of the organism in ecology, development, and evolution. One way to do so is to highlight the special explanatory role that the category of agential niche construction can play, which is the strategy of the rest of this chapter. To begin, let us examine teleological explanations in general. A teleological explanation explains something in terms of its purpose. According to Walsh (2015), teleological explanations point out regularities or dependencies between *means* and *goals* that we do not capture in standard sequential causal-mechanistic explanations. To illustrate this, think of the difference between encountering a friend downtown by chance and a planned meeting. In the case of encountering the friend by chance, seemingly innocuous changes to the initial conditions might preclude the encounter from happening. For example, window shopping for a just a moment is enough for the encounter to not happen. In chance occurrences, a detailed account of the mechanisms which brought about the occurrence (and the relevant initial conditions) sufficiently explains the occurrence. In contrast, a planned meeting will occur across a broad range of initial conditions and across a broad range of mechanisms which realize the occurrence. You might go by car, bus, or by foot; you might be late or early; you might travel from work, home, or anywhere else. Either way, you will most likely end up encountering your friend, *because* that is your goal.

Thus, an explanation merely citing the sequential mechanisms which realize your encounter leaves out an explanatorily salient regularity—the fact that an encounter with your friend is the *goal* and that a completely different sequence of mechanisms could equally realize the encounter. This regularity stems from the dependence of *means* on *goals*. The *goal* is available across a range of different *means*. In this case, a teleological account of the occurrence explains why *it was not a chance occurrence*. Teleological explanations might thus uncover regularities which, on a purely mechanistic account, would be considered the result of "blind" chance or variation. To neglect, reduce, or otherwise explain away teleological regularities might lead to what Walsh (2015, 194) calls a "selective blindness to a whole class of explainable regularities." Thus, by allowing teleological language to refer real and empirically tractable relationships, instead of treating it as terminological shorthand that ultimately can be reduced and translated into the effects of prior selection or intentional deliberation, we open up a whole class of potentially underappreciated explainable regularities.

An example of such a regularity can be seen in the results of a meta-study of hundreds of selection gradients measured in natural populations of different species by Clark et al. (2020). The meta-study shows that environmental variation that is buffered by organismic activity (e.g., nest building, pupal cases, burrowing) generally results in reduced variation in selection gradients and weaker directional selection relative to non-buffered (or non-constructed) environmental variation. This is line with how niche construction is argued to alter the conditions of selection to favor traits that are beneficial to organisms controlling and regulating environmental variation through their activities instead of favoring traits that directly address environmental heterogeneity (e.g., Laland et al. 2017).

The reason why this should be seen as an example of a regularity that is uncovered by a teleological account is that it points to a general dependence of *means* on *goals*, which holds across a wide array of taxa. What are environment-buffering activities *for*? The evidence suggests that organisms engage in such activities *in order to* reduce environmental variation. This regularity also helps explain how goal-directed behaviors can influence selection. Environment-buffering activities influence selection gradients by reducing environmental variation. The reduction of environmental variation in turn alters the selective environment to favor traits that are useful for regulation and control of heterogenous environmental factors. This means that not only does selection favor environment-buffering traits because they have been beneficial in the past, but also because the selective environment has (partly) been constructed by the environment-buffering activities themselves. Thus, if we try to reduce teleological explanations to causal-historical explanation—as for example the selected-effects of priori selection (Millikan 1984; Neander 1991)—we might gloss over the fact that the prior selective environment was itself partly the result of the very purposiveness that the selected-effects approach is supposed to account for by citing the prior action of selection. Instead of treating the purposiveness of organisms exclusively as an *explanandum* (as one does in the reductive approach to teleology), we should allow such teleological relationships to serve the role of *expalantia*, especially in cases where we can observe goal-directed behavior.

7.6.1 The Origins and Possession of Goals

Now that we have accounted for why non-reductive teleological explanations can be important, and what the explanatory roles of means and goals are, we need to account for what goals are and where they come from. A goal is a stable end-state of system and goal-directed processes are processes that aim to bring about and maintain those end-states (Walsh 2015). Organisms are engaged in goal-directed behaviors when their behaviors are directed at and conducive to a certain end-state. Another way to say this is to say that organisms exhibit *purposiveness*. But does the attribution of *purposiveness* to an organism also entail further capacities such as foresight, deliberation, or other higher-order mental capacities in the goal-seeking organism? I do not think so. In attributing a goal to a behavior, we do not have to simultaneously attribute any form of knowledge of the goal in the organism itself. For example, in case of the leaf-altering plant discussed above, the goal of the behavior is "to increase light capture". An individual plant would indeed have to be endowed with quite a sophisticated mental life to be able to understand *why* it performs the behavior, *why* the behavior is conducive to a certain goal, or even *that* the behavior it performs has a specific goal. Fortunately, the goals of behaviors exhibited by organisms do not have to have correlated mental state in the organisms exhibiting it. It is sufficient that reaching the goal increases the relative reproductive output of the behaving organism. A similar argument is provided by Laland et al. (2019) in their discussion of purposiveness as a fundamental feature of life:

> When we assert that organisms are "purposive" we mean nothing more than that organisms exhibit goal-directed activities such as foraging, courtship, or phototaxis, which are entirely natural tendencies with short-term local objectives, and that have themselves evolved. The "goals" and "purposes" to which we refer can be defined with respect to general aspects of biological function, such as resource acquisition, stress avoidance, and reproduction. (Laland et al. 2019, 132)

So, having a goal does not require foresight or any other complex cognitive capacities on behalf of the organism. However, we also need an account of where goals come from. A common strategy in providing a naturalistic account of goals is to highlight the autopoietic nature of life (Varela et al. 1974). This refers to the fact that an organism is a "self-building, self-regulating, highly integrated, functioning, and (crucially) "purposive" wholes, which through wholly natural processes exert a distinctive influence and a degree of control over their own activities, outputs, and local environments" (Laland et al. 2019, 132). Thus, goals arise in virtue of organisms needing to actively maintain their internal order and dynamic stability to stay alive. The simplest goal-directed processes thus have self-maintenance as the end-state they are directed at. More complex goal-directed behavior follows from organisms evolving more capacities (increased morphological, physiological, and behavioral complexity) which consequently increase what opportunities their environments afford them (Walsh 2015). Thus, a perfectly naturalistic account of goals and purposiveness is readily available.

7.7 Potential Issues with the Agential and Contributional Distinction

Now that we have established that there is a distinction between agential and contributional niche construction, and that organisms across the tree of life can exhibit goal-directed behavior, let us turn to some potential issues. First, there is the question whether and how groups can engage in *collective agential* niche construction. Second, how does the agential and contributional distinction relate to the difference between constructing one's own niche and constructing that of others? Finally, while agency requires goal-directedness, not all goal-directed processes are instances of agency. What are we to make of non-agential, yet goal-directed, processes?

7.7.1 Can Groups of Organisms Engage in Agential Niche Construction?[40]

Niche construction often happens through the activities of multiple organisms. In the case of contributional niche construction, this is relatively unproblematic since it is simply several organisms that are doing the same thing. Thus, the effects of group-level behavior will most likely increase in proportion to group size. There might be cases in which the group size has to be large for the effects of niche construction to be significant, as in the case of cyanobacteria or cross-feeding bacteria.

However, agential niche construction at the level of a group seems more problematic. How are we to account for groups that engage in goal-directed behaviors? On this matter, I suggest we look at an analogous discussion in action theory. In action theory, collective agency is generally seen as action performed by individuals in virtue of a shared goal and (often) a joint commitment to the reach the goal (Gilbert 2010).[41] A contentious debate concerns whether or not going beyond the goal of the individual is necessary for collective action. For some, it is sufficient that individuals share a goal and act as a group (e.g., Bratman 1993). In such a case, a group-level action could simply be the aggregation of the individual-level behaviors. Obligate shoaling in fish is a good example of this kind of collective goal-directed action. The individuals share a goal (e.g., "staying close to conspecifics for safety") and act as a group. The group-level shoaling behavior is simply a function of individuals performing behaviors directed at a similar individual-level goal. It is not the goal of the group to perform shoaling behavior. Shoaling behavior is rather a consequence of the individuals performing behavior directed at their individual, though *shared*, goals.

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[40] I would like to thank Jan Baedke for pointing out this problem when I presented an earlier draft of this chapter at ISHPSSB 2019.

[41] It is common to talk in terms of *shared intentions* and not *shared goals* in philosophy of action, as it is primarily concerned with human social interaction. I use the term 'goal' in order to avoid the question of intentionality. The reader can interpret this paraphrasing as a "minimal" reading of the positions in action theory whose purpose is merely to illustrate differences between group behaviors in non-human organisms that exhibit varying degree of behavioral complexity.

However, there are some in philosophy of action who argue that a joint commitment to reach the goal is necessary for collective action (e.g., Gilbert 1989). What this means is that the shared goal is attributed to the group, and not simply to the individuals. A consequence of a goal shared at a group level is that the group-level behavior is no longer simply an aggregate of individual-level behavior, but rather a function of potentially varying individual-level behaviors each serving a role in the attainment of the shared group-level goal. Complex hunting strategies in social animals or the different behaviors and morphologies of ants from different castes in a single colony are example of collective agential niche construction in which the goal is shared at a group-level. What differentiates this kind of collective action from aggregate action is that it the requires a minimal degree of orchestration amongst individual behaviors to reach the shared group-level goal. In social hunting, an indication of this type of orchestration is the possibility of certain individuals correcting other group members when they fail to perform the appropriate behavior necessary for achieving the shared group-level goal. Thus, collective agential niche construction can be grouped in two categories. As *aggregated* and *orchestrated* collective (goal-directed) action. Aggregated collective action occurs when group members have similar individual goals and act as group. Orchestrated collective action are cases in which the goal is shared at a group-level. Whether or not different instances of group-level agential niche construction is aggregated or orchestrated, and what mechanisms are responsible for such orchestration, is an empirical question which should be solved on a case-to-case basis.

Another potential problem for collective agential niche construction concerns groups of interspecific organisms which seemingly act collectively, such as a holobiont. Could such groups of organisms be said to have the capacity for agential niche construction as a super-organism? The complexities of the interactions between the different species that compose a holobiont (e.g., differences in temporal and spatial organization) provide a significant obstacle to the attribution of a shared goal, both at the individual and group level. In the case of a holobiont, it seems unlikely that a eukaryotic host and its microbiome can share a similar goal, unless we construe that goal in a very general manner, e.g., as "the goal of self-maintenance" discussed above. This option, however, is equally open to entire ecosystems, which are composed of interacting organisms, all of which (except the very melancholic of us) share the goal of self-maintenance. Are ecosystems a reasonable locus for collective action? It seems somewhat strange to attempt to attribute agency to something simply by alluding to the fact that life is interconnected and that organisms generally aim at self-maintenance.

7.7.2 Agential Niche Construction of a Different Species' Niche.

At first glance, it might seem that agential niche construction is limited to the construction of the organism's own niche. However, there are many examples of goal-directed behavior that aims at manipulating another species' environment. An obvious example of this comes from cultivation and domestication of plants and animals by humans (Piperno 2017; Smith 2007, 2016; Zeder 2016). In such cases, the niche of the domesticated organism is (partially) constructed by the domesticating organism. Such practices are not limited to humans, however. There are several instances of ant-fungus mutualisms where ants cultivate fungi in their colonies as a food source.[42] The most studied species of fungus-cultivating ants are the leaf-cutter ants. These are commonly referred to as "higher" attines because they cultivate highly derived fungi which have no wild-type counterparts, and they form obligate mutualisms. These ants actively propagate, nurture, and defend different species of fungi of the clade *Lepiotaceae*. The fungi benefit from a steady supply of nutrition in the form of fresh plant matter and protection against pests and mold, while the ants in turn feed on the nutrient-rich hyphal swellings of the fungi called the "gongylidia" (Chapela et al. 1994).[43] In this case, we would say that the ant is engaged in agential niche construction of another species when it performs behavior such as cutting fresh plant material and placing it in close proximity to the fungus so that the fungus can excrete digestive enzyme and absorb the nutrients from the plant material. In other words, the ants cut fresh plant material and place it close to fungus *in order to* provide nutrition to the fungus.

Thus, in cases of cultivation and domestication, there are organisms engaged in agential niche construction of a different species' niche. However, cultivation can also

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[42] Cultivation of fungi have been found in termites as well, so agricultural practices in eusocial insects is more prevalent than just amongst different species of the tribe *Attini*, which is by far the most studied (Mueller et al. 2005).

[43] There is much more complexity to ant-fungus mutualism. For example, there is mounting evidence that a host of microbial organisms, e.g., gut-bacteria in the ants, are intertwined in these mutualistic relationships (Aylward et al. 2012).

happen *indirectly*. What are we to make of such cases? In such cases it might not be clear whether an organism is engaged in agential or contributional niche construction. An example can be found in the male spotted bowerbird, *Chlamydera macultata*. These birds are famous for their elaborate bowers used primarily as displays to attract mates. A recent study found that male spotted bowerbirds use the fruit of a species of nightshade (*Solanum ellipticum*) as an important part of their sexual display (Madden et al. 2012). Males that have many fruits on display (and consequently in and around their bowers) experience high mating success. However, when the male birds arrive at new sites with unconstructed bowers, they do not choose sites with a higher number of *S. ellipticum* plants than any other random site suitable for bower construction. Most male bowerbirds are also relatively sedentary, occupying the same bower for periods up to 10 years and remain close to their previous year's bower site (sometimes less than 10 meter). Finally, there is no evidence that the fruit is consumed or serves any role beyond ornamentation during sexual displays.

The male spotted bowerbird benefit from a local supply of *S. ellipticum* fruit in two ways. First, by being able to easily maintain a high number of fruits in their bowers being readily available during sexual displays, thus increasing the chance of mating success. Second, males that have many fruits in their bowers experience an increase in *S. ellipticum* plants in the following year, and consequently more fruit readily available for future sexual displays. Madden et al. (2012) also speculate that a third way the male spotted bowerbird might benefit from having a local supply of *S. ellipticum* fruit is by having to spend less time foraging away from their bower, thus reducing the risk of marauding neighboring rivals. The *S. ellipticum* plant, being a perennial pioneering species, benefits from being collected by the bower birds in virtue of being deposited in areas with little surrounding vegetation, which is favorable for seed germination and pioneer establishment.

The use of these fruits in sexual displays have thus resulted in male spotted bowerbird *indirectly* cultivating *S. ellipticum* plants. The reason why this is referred to as indirect cultivation is that Madden et al. (2012) have found no evidence that the bowerbirds engage in any sort of soil manipulation or other activities that would increase the fruit yield or germination success of *S. ellipticum*. They instead argue that it is most likely a by-product of males removing fruit that has turned brown from their displays and drop them in the immediate vicinity of their bowers. In other words, there is no evidence that *S. ellipticum* cultivation is a result of behavior *directed at* cultivation.

In the case of the spotted bowerbird, the male is engaged in the construction of his *own* niche—i.e., the construction of the bower for use in sexual displays. But he is also engaged in the construction of the niche of a number of *S. ellipticum* plants by inadvertently relocating seeds so they experience different selection pressures (e.g., high fruit yields become a more favorable trait than traits associated with resource competition). If there is no evidence that there is any goal-directed behavior behind the bowerbirds' cultivation of the *S. ellipticum*, it would seem to be a case in which the bowerbirds are engaged in both agential (constructing elaborate bowers that function as a stage for sexual displays) and contributional niche construction (relocating *S. ellipticum* seeds inadvertently to novel selective environments). However, it would be wrong to argue that this is the case since in one instance the bowerbird constructs its own niche, while in the other it is constructing the niche of a different species. Had the male bowerbirds, for example, carefully managed soil patches around its bower where it discarded the *S. ellipticum* fruits that had turned brown, and the best explanation of this is that it did so *in order to* increase the fruit yield the following year, then both the bower construction and the fruit relocation would be *agential* niche construction.

For the *S. ellipticum*, the resulting evolutionary dynamics of being either *indirectly* or *purposively* cultivated—i.e., as consequence of either contributional or agential niche construction—might be similar. However, it doesn't have to. If the male bowerbird began to purposively cultivate *S. ellipiticum*, the plant might lose some of its pioneering traits and start evolving typical domesticated traits such as larger fruits or reduced branching.

Is the cultivation of *S. ellipitiucm* plants in fact the result of goal-directed behavior or just a byproduct of their sexual display? Madden et al. (2012) argue that there is no evidence that the cultivation is a result of goal-directed behavior. Thus, until more evidence is gathered, and we see a good reason to revisit the question of whether or not the cultivation is a result of goal-directed behavior, no teleological explanation of the niche constructing activity is necessary. It is sufficient to point out that *S. ellipticum* is a pioneering species and that the conditions which seeds, and seedlings are exposed to when relocated by the male spotted bowerbird are favorable for pioneering species. Consequently, *S. ellipticum* plants tend to proliferate around bowerbird nesting sites.

Many instances of mutualisms are thought to start out as one species being exploited by another (Conner 1995; Odling-Smee et al. 2003). Such cases begin as contributional niche construction, but as the exploited species begins to exploit its exploiter, a mutualistic relationship evolves. Such cases are likely to end up as agential niche construction, at least in the case of the original exploiting species (e.g., the leaf-cutter ants discussed above, and it seems to be true for most cases of domestication). A distinction between contributional and agential niche construction can be helpful in describing the way in which some mutualisms end up as instances of domestication, and how goal-directed behaviors of agential niche construction might alter the selective environment in a different manner than what would we expect from contributional niche construction.

7.7.3 Teleology does not equal Agency

So far, we have understood agential niche construction primarily in terms of goal-directedness. However, not every goal-directed process counts as an instance of agency. Goal-directedness is usually taken as a necessary, but not sufficient, condition for the attribution of agency. Agency is thought to require something more, namely an influence of the agent over the behavior it performs. In action theory, Frankfurt (1998) defends a position in which agency consists in goal-directed behavior which is under the *guidance* or *influence* of the agent—alternatively as goal-directed activities over which an organism exerts a *degree of control* (Laland et al. 2019). Organismic agency can thus be seen as the capacity of an organism for goal-directed behaviors over which (to a lesser or greater extent) the organism itself exerts a degree of control. Agential niche construction, then, are cases in which the niche constructing behavior is goal-directed and where the organism performing it exerts a degree of control over that behavior.

A potential counterexample would be cases in which organisms perform goal-directed behaviors over which they exert no control. One such example could be behaviors that are thought to be genetically predetermined, where the prior action of selection on genetic variation have produced behavioral programs over which the organism has no influence. Historically, burrowing and nest building behaviors have been described as genetically determined, although recent studies have revealed considerable plasticity in such behavior (e.g., Hansell 2007). However, even if there is a strong degree of genetic determination on such behaviors, it does not follow that an organism can be said to exert no influence over the behavior. If the behavior is directed at the alteration of the environment, it is likely that the organism will be sensitive to a whole range of conditions that requires an alternate behavioral output for the alteration to obtain.[44] As a simple example, think of an organism attempting to construct a burrow in a surface that is too hard to penetrate. It will, most likely, after a short while attempt to burrow in a different location where the surface has different properties. A staple of goal-directed behavior is that it is subject to adjustments that compensate for the effects that different circumstances generate in the normal course of the behavior while retaining its original goal (cf., persistence and plasticity in Lee and McShea 2020). This fits well the *affordance* approach to agency introduced above. It is not necessary that an organism enjoys a large degree of behavioral flexibility (i.e., possesses a large repertoire of capacities) for it to be capable of agency. It could have a relatively limited set of capacities in its repertoire—and consequently fewer affordance to respond to—while still exerting an influence or control over its behavior. Thus, a large degree of behavioral flexibility is not necessary for organismic agency, but rather an indication of the degree to which an organism enjoys freedom of action in pursuit of its goal. Freedom should here be understood not in terms of volition, but rather as possessing different *means* to deal with impediments and opportunities for achieving a goal.

What about instinctual and reflexive behaviors? Such behaviors are not under the control or guidance of the organisms performing them, yet clearly exhibit goal-directedness. If stimuli elicit reflexive or instinctual responses, the whole point in referring to those responses *as* reflexive or instinctual is to indicate that they are *outside* the control of the organism. Such behaviors seem to show that there is a potentially large group of goal-directed behaviors which are not instances agency, so why not think that most goal-directed behaviors are instinctual or reflexive? Presumably, this is how we need to conceive of genetically predetermined behaviors if they are *not under influence* of the organism. Most organisms, however, exhibit the capacity to *overcome* inappropriate or unnecessary reflexive and instinctual responses through habituation, desensitization, plasticity, or other forms of learning and experience

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[44] More likely, a behavioral disposition for engaging in nest building would be what is under genetic control, while the actual nest building behavior is under the influence of the organism as it interacts with its environment.

(Ginsburg and Jablonka 2019). Habituation has even been observed in non-neural organisms, such as the flowering plant *Mimosa pudica* (Gagliano et al. 2014) and in slime molds (Boisseau et al. 2016). Thus, while instinctual and reflexive behaviors certainly occur in most—if not all—organisms, the ability to rectify such behaviors when unnecessary or inappropriate is what is indicative of agency. In such cases, the control or guidance of the behavior is not concomitant with the performance of the behavior, but rather exerted a later stage as a consequence of learning or experience.

Finally, what are we to make of goal-directed processes of sub-organismal parts? For example, pupil dilation and constriction, or the vertebrate cardiac cycle are goal-directed process, but we usually do not consider those as instances of agency. Rather, these processes are often conceived as *automatic* and contrasted with agency. However, such processes can be *indirectly* influenced by the activities of an agent as *whole.* Animals that feed infrequently and in large portions often indirectly influence digestion by staying stationary after feeding allowing more blood to go to the digestive system rather than to their extremities. Many mammals without fur use mud to influence thermoregulation. Both thermoregulation and digestion are *automatic* goal-directed processes, and consequently not instances of agency. However, if the organism has the appropriate behavioral capacities and the environment affords the right opportunities, the organism as a whole can influence such processes indirectly. Just as with reflexive and instinctual behaviors, there can be processes within an organism that are goal-directed yet automatic, without this surrendering its status as an agent.

Thus, attempting to undermine the attribution of agency to an organism by referencing teleological processes that are not under the influence of the organism is likely to ultimately result in a view in which all behaviors must be instinctive, reflexive, or automatic, unless the organism has a capacity for deliberation or intentionality. Such a view runs counter to what we observe in typical goal-directed behaviors, namely persistence and flexibility (or plasticity). Persistence and flexibility together are good indicators that the organism performing the goal-directed behavior exerts some degree of influence or control over the behavior, and consequently can be treated as an *agent.*

7.8 Conclusion

In this chapter we have seen that the concept of niche construction has been conceived and defined in several different ways reflecting the theoretical utility of the concept across a broad range of phenomena and disciplines. I argued that there is an important distinction to be made between *agential* and *contributional* niche construction. The distinction is fleshed out in terms of *goal-directedness*, where agential niche construction is the product of goal-directed behavior while contributional niche construction is not. In instances of agential niche construction, an account of *why* the niche construction occurs requires a teleological explanation to fully appreciate how organisms are active participants in development, ecology and evolution as *agents*. In instances of contributional niche construction, a teleological explanation of why the niche construction occurs does not have any bearing on the organism's role as *contributors*. The distinction is important because asking whether an instance of niche construction is agential or contributional (or both) can potentially uncover novel explainable regularities and phenomena that might otherwise remain unidentified. Further, interpreting niche constructing behavior as *agential* allow us to use niche construction theory to highlight important instances in which organisms across the tree of life (in bacteria, fungi, plants and animals) exhibit agency and get a better grasp on how organismic agency influences evolutionary, developmental, and ecological processes, such as natural selection.

8

CONCLUSION

The common thread throughout these chapters has been the focus on organism-environment interactions and their role in evolutionary theory. As we have seen, organisms and environments are usually treated as a duality in evolutionary theory. In chapter 2 I suggested that this is a mistake. Rather organisms and environments are inextricably linked—codependent and codetermined. There cannot be environments without organisms inhabiting them, and there cannot be organisms without environments to sustain them. Further, organisms and environments determine each other's properties. The features of organisms define and constrain what aspects of the physical surroundings that are environmental factors. Likewise environmental factors define and constrain the possible phenotypes of a population. The codetermination and codependency of organisms and environments have consequences for how we understand evolutionary theory and its concepts. Adaptations, commonly defined as a feature or property of an organism, cannot be regarded as adaptations unless they stand in a functional relationship to environmental factors. Natural selection, commonly seen as an environmental process that discriminates between different phenotypes, is rather a process that discriminates between the outcomes of organism-environment interactions. Finally, biological evolution, narrowly understood as the changes to the allele frequencies in a population over generations, and broadly understood as the changes in the proportions of different phenotypes in a population over generations, should rather be seen as the changes in the proportions of different organism-environment relationships in a population over generations. The fundamentality of organism-environment interactions in biology points to a causal parity between environmental factors and organismic activity in shaping the selective environment and consequently the action of selection. This contrasts with externalism—the view that selection pressures are formed by environmental factors alone and that natural selection consequently is an environmental process—and opens up the possibility for organisms to play an active role in evolutionary theory.

8.1 Natural Selection and the Active Role of the Organism

The activities of organisms, on an asymmetrically externalist approach to evolutionary explanation, can only play the role of *explanada* (that which is being explained). Since natural selection is conceived as an environmental process that eliminates non-beneficial phenotypes and retains beneficial ones in virtue of genetically inherited parent-offspring similarity in phenotypic expression, the activities of organisms are conceived to be largely (though not exclusively) a matter of genetic disposition resulting from the prior action of selection. Consequently, a worry for the asymmetrical externalist is that in allowing the activities of organisms which are not the result of genotypic variation to influence evolutionary outcomes and play the role of *explanantia* in evolutionary outcomes, we come uncomfortably close to allowing for Lamarckian evolution through acquired characteristics. As such, the organism is relegated to the role of an object, and not a subject or agent, in evolution. This apprehension is due to the false idea of the organism and environment as being a duality. If we instead adopt the view that organism-environment interactions are fundamental, we can circumvent this apprehension and allow for organisms to play an active role as subject and agent in evolutionary theory. In chapter 3, I argued that natural selection is an *ecological* process, it acts on the outcomes of organism-environment interactions and is not sensitive to the systems of inheritance responsible for the reoccurrence of those interactions in subsequent generations. On this view, we saw that organismic activity can in fact influence evolutionary outcomes without being the result of prior action of selection and consequently play the role of *explanantia* in evolutionary explanations. In chapter 4 I showed how, by viewing natural selection as an ecological process, we can incorporate niche construction as one way in which an organism can achieve a fitness advantage relative to other members of its population and consequently be favored by natural selection. In chapter 5 I argued that the proximate-ultimate distinction is perfectly compatible with organismic activity and other individual-level developmental and ecological processes having a causal role in evolutionary outcomes, and consequently in being considered *ultimate* causes in evolutionary explanations of such outcomes. However, organismic activities and other individual-level developmental and ecological processes can only be regarded as ultimate causes if they structure or influence the action of population-level processes or outcomes, such as the action of natural selection.

I hope in these chapters to have shown that by adopting a view of natural selection as an ecological process—which is motivated by the codependency and codetermination of organism and environment—we can allow the organism to play an active role in evolution without abandoning or revising the central theoretical framework of evolutionary theory.

8.2 Niche Construction Theory and its Place in Evolutionary Theory

In the final two chapters I offered specific arguments in relation to niche construction theory. Niche construction theory is a conceptual and theoretical framework which attempts to demonstrate both the validity and utility of viewing organisms as agents in evolutionary theory (Laland et al. 2019). I have argued that niche construction theory can be conceptualized in a manner that is perfectly compatible with standard evolutionary theory. On this view, niche construction should be seen as a theoretical supplement, rather than a revision, to evolutionary theory. I also argued that niche construction theory should have a broader conceptual framework than what is offered in the canonical treatment of niche construction in niche construction theory. Developmental processes like learning, phenotypic plasticity, or behavioral innovation, can all be conceptualized as mechanisms which allow an organism to engage in niche construction, if they engender changes a selective environment. Niche construction theory is one of the most well-developed conceptual and theoretical frameworks for studying the active role of the organism in ecology and evolution. I hope to have shown that it is perfectly compatible with standard evolutionary theory and deserves to be an integral part of it.

Finally, I have argued that a distinction between agential and contributional niche construction can help naturalizing the concept of teleology and allow for non-reductive teleological explanations in evolutionary biology. I also argued that the category of agential niche construction can be helpful in showing how the capacity for agency might be widespread across the natural world. The capacity for agential niche construction also allows the sources of selection (i.e., selection pressures/ selective environments) to originate from goal-directed processes. This, I think, is the most controversial part of my thesis and I will conclude my dissertation with a short epilogue attempting to dowse some of that potential controversy.

8.3 Epilogue – Natural Selection and Organismic Agency

The pride and joy of Darwinian evolutionary theory (natural selection and common descent) is that the apparent purpose and design of well-adapted organisms in an otherwise purposeless universe can be explained without having to invoke providence or a designer, but rather through the purposeless process of natural selection. I wish to emphasize that my defense of non-reductive teleology to no extent mean that I think or imply that there is any kind of purpose or design *inherent* in the process of natural selection. Rather, natural selection, as I have argued throughout this dissertation, is a process that iterates successful organism-environment interactions when possible. If an organism exerting a degree of flexibility and control over its behaviors makes for a successful strategy, then natural selection will, whenever possible, iterate that strategy. In a population of organisms that vary in the degree of freedom they exert over their behaviors (i.e., behavioral flexibility) and in their capacity for learning, those individuals are potential objects of selection (given that these capacities produce *actual* adaptive responses in an environmental context). That much is uncontroversial. If the degree to which the organisms vary in behavioral flexibility and capacity for learning generate difference in relative fitness and is heritable, then there can be directional selection on those features. Still pretty uncontroversial. With a relatively large degree of freedom (or flexibility) over one's behavior and a broad capacity for learning, an organism can learn to do stuff for the sake of a certain result within their lifetime. In other words, they can learn or discover particular means-end relationships. If discovering such means-end relationships engender an increased relative fitness, and the capacity to learn or discover those means-end relationships are transmitted to the subsequent generations, then natural selection will favor the *acquisition* and consequent *exploitation* of such means-end relationships. At this point, directional selection can happen in (at least) one of two ways. Either by increasing the ease of acquiring the means-end relationship, or by increasing the capacity to exploit a wider range of means to reach the appropriate end-state. In the first case, there will probably be a small number of means that are easily obtainable and consistently guide the organism to the appropriate end-state. In such cases there will be selection against learning and selection for instinctual behavior (i.e., selection against behavioral flexibility and learning). The Baldwin effect discussed in chapter 3 is potentially a good example of this process.

In the second case—in which selection favors organisms that have the capacity to exploit a larger variety of means to reach the end-state—selection will favor more freedom of behavior (behavioral flexibility) and a keener capacity for learning. Those capacities are presumably much harder to transmit to subsequent generations, so the directionality of selection will probably never be as strong as in the case of genetic accommodation.[45]

However, in both cases, the selection pressures originate with the agential capacities of the organisms—with the acquisition and exploitation of a means-end relationship. Natural selection can subsequently restrict or extend the agential capacities of the organism (behavioral flexibility and learning). In either case, there is selection for goal-directedness, as instinct or through agency, and the selection pressures *originate* from a goal-directed process. Thus, trying to reduce the teleological content in an explanation of such outcomes to the prior action of selection will only partially account for the outcome. The selection pressures themselves are the result of *something that was learnt*—viz., the acquisition of an *actual* means-end relationship. Thus, by natural selection favoring behavioral flexibility and learning, it also expands the possibility of novel selection pressures that result from those capacities. Such capacities will often discover novel means-end relationships, and the

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[45] This might partially explain the ubiquity in the natural world of behaviors that, at least at a first glance, seem to be instinctual. While examples of organisms exhibiting a large degree of behavioral flexibility and learning are much rarer products of natural selection.

manner in which the organism acquires and exploits these will subsequently be what constitute (parts) of novel selective environments.

By allowing teleology to play an explanatory role in accounting for the sources of selection, all I really argue is that in virtue of natural selection producing organisms with certain capacities, especially behavioral flexibility and learning, natural selection enabled novel selection pressures to be produced by such capacities, some of which are *teleological* in nature. There is thus a selection-based explanation of how a purposeless process (i.e., natural selection) have produced organisms which themselves can introduce purpose into that process.

Consequently, I do not think that the arguments presented in this dissertation warrant any kind of talk of an overarching purpose, design, or creator of the natural world. But they do let us take seriously the thesis that organisms should be considered *agents* in evolutionary theory, and that the capacity for *agency* can be seen as a product of natural selection which itself can influence the action of selection in a goal-directed manner.

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