Natural Selection and the Unity of Functional Analyses*

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While the question of whether selected-effects accounts of function or causal-role accounts of function provide the 'true' functional analysis has given way to a general pluralistic consensus, Philip Kitcher has suggested that different functional accounts allow for unification. I argue that Kitcher's attempt to unify the two functional analyses fails because he adopts the environment-centered perspective on selection as a premise. The premise is undermined by the role niche construction is likely to play in the context of evolution. Moreover, I raise the tentative suggestion that niche construction may threaten the applicability, or at least the relevance, of selected-effects ascriptions.

1. Introduction. Since the publication of two seminal papers on the subject of functional explanations—one by Wright (1973), the other by Cummins (1975)—in the 1970s, two strands of functional explanations have evolved: etiological accounts that purport to identify 'proper functions' on the basis of Wright's theory and causal-role accounts based on Cummins's theory. Over the last 3 decades, a large number of philosophers of science have attempted to defeat one of these two accounts and to defend the other. Even though the academic quarrel has not been settled yet, more recently there has been a tendency toward an acceptance of the view "that these two concepts are in the service of different explanatory projects in biology—*proper function* at work in evolutionary theory and behavioral ecology to explain the presence of a functional trait in its bearers, and *Cummins function* at work in physiology and developmental biology to explain the causal contribution of a functional item in a complex process" (Buller 1998, 514). This position implies the concession that there is no one 'true' account of functions. Both etiological and causal-role accounts

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are valid. Which one will be the more adequate to employ depends on the task and context at stake. This view has been defended by, among others, Godfrey-Smith in an article suggestively titled "Functions: Consensus without Unity" (1998). This article is largely a response to and criticism of Philip Kitcher's attempt to provide an account that merges both of these explanatory enterprises. At the heart of Kitcher's project lies the notion of design, with natural selection being the source of design in a biological context. In this essay, the main target under attack is Kitcher's adoption of an environment-centered perspective of natural selection on which his argument for the "idea that there is some unity of conception that spans attributions of functions across the history of biology and across contemporary ascriptions in biological and non-biological contexts" is based (1998, 258).

2. Plan of Action. I commence with an exposition of causal-role and etiological functions and touch on some of the difficulties with which each of them struggles. In doing so, I want to motivate the sense that neither of these two accounts somehow outdoes the other. Rather, we have reason to believe, as Godfrey-Smith put it, that "we should accept both senses of function, and keep them strictly distinct. All attempts to make one concept of function work equally well for behavioral ecology and physiology are misguided. On this view, 'Wright functions' and 'Cummins functions' are both effects that are distinguished by their explanatory importance. The difference is in the type of explanation" (1998, 285).

Subsequently, I provide a summary of Kitcher's argument before I embark on my line of attack against this argument. My criticism is directed against Kitcher's adoption of what he calls the "environment-centred perspective on selection" (1998, 261), on which his argument rests to a large extent. I argue that Kitcher either sidesteps or disregards worries concerning the role of niche construction in evolution. If Kitcher's argument rests on the environment-centered perspective on selection, then, given recent developments in niche-construction theory, there is a problem that might pull the rug out from under Kitcher's argument. In addition, I suggest that one might develop worries about whether the applicability of etiological functions might possibly be jeopardized if natural selection does turn out to play less of a role in evolution than is commonly suggested. Etiological functional analysis is conceptually tightly linked to adaptationism. Adaptationism in turn has the tendency to regard environments as fixed, even in the long term, and as autonomous from organisms inhabiting them. Moreover, it regards natural selection as the paradigmatic evolutionary force. The empirical adaptationist program has already been challenged from various sides, perhaps most notoriously by Gould and Lewontin, by pointing to the importance of evolutionary forces

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and constraints other than natural selection. It might yet be forced to more modesty if niche construction turns out to be as prevalent and evolutionarily consequential as has been suggested by scholars such as Odling-Smee, Laland, and Feldman. The weaker the adaptationist program, the less we may have to say from a selected-effects point of view on the matter of biological functions.

3. Wright versus Cummins. Wright provides a neat and simple definition of function:

> The function of *X* is *Z means*
>
> (a) *X* is there because it does *Z*,
> (b) *Z* is a consequence (or result) of *X*'s being there. (1973, 161)

This definition makes no reference to natural selection, but it already incorporates the idea "that the function of an entity is what explains why that entity is there" (Kitcher 1998, 264). Despite, or perhaps because of, its appealing simplicity, Wright's account of what a function is has been confronted with cases that make it look too inclusive. Godfrey-Smith cites an example provided by Boorse, which is meant to bring out this too-inclusive nature. This example concerns a small rock holding up a bigger rock in a fast-moving stream. "If the small rock did not support the larger rock, it would be washed away. Holding up the big rock is what the small rock does; that explains why it is there. So on Wright's original analysis this is the function of the small rock" (Godfrey-Smith 1998, 282–83). This conclusion seems unintuitive, if not to say wrong. Hence, in order to avoid cases like these, it has been suggested, perhaps most notoriously by Ruth Millikan (1989), that a further criterion should supplement Wright's analysis: for something to be called a function, a trait X must have been favored by natural selection exactly for X's doing or performing Z. Adaptive traits are selected for their effects. Not surprisingly, etiological accounts are also referred to as 'selected-effects accounts'.

On Cummins's account, "to ascribe a function is to ascribe a capacity to it which is singled out by its role in an analysis of some capacity of some containing system" (1975, 765). Functions are not primarily defined in terms of the (evolutionary) reasons for their existence but in terms of their (causal) contribution to a system's particular capacity. Buller succinctly contrasts the two accounts by saying that "ascription of a proper function purportedly answers a question about why the functionally characterized item is present in its bearer, while ascription of a Cummins function purportedly answers a question about how the functionally characterized item contributes to a feature of its bearer" (1998, 514). Thus, the existence of tongues (e.g., across different species) may possibly be

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explained in reference to food-processing-relevant effects. On a Cummins account, though, we can provide a functional analysis of how the tongue contributes to the processing of food causally speaking (although in this context there is no claim as to why tongues exist). Similarly, we can give a Cummins account of what the function of the tongue with respect to speaking is, although the tongue's existence was not selected for because of its effects on speaking. Hence, while the tongue has one function according to the selected-effects account, its role in food processing, it has at least two (although there are certainly many more) functions viewed from Cummins's point of view: its causal contribution to both food processing and speech in humans.[1]

4. Is There One 'True' Account of Functions? The Case for Pluralism. A number of reasons have been provided for regarding selected effects as the 'true' kind of functions. The four most compelling and salient ones follow.

1. Selected-effects accounts help us to identify proper functions as opposed to accidental benefits. "Something can have beneficial effects, or make a useful contribution to a containing system, but these are not functions unless the thing in question is there because of these effects. Otherwise they are accidental, fortuitous benefits" (Godfrey-Smith 1998, 282). If we know the proper function of a trait, we know why the trait exists.
2. Wright-style functional accounts that appeal to natural selection do not suffer from promiscuity as Cummins functional accounts do. The argument is that Cummins's theory allows for functional attributions in cases that run counter to what should (at least intuitively) count as a function. Thus, the causal-role account is seen to allow us to regard rain clouds as functional in the context of the hydrologic cycle, and green plants can be seen to function as regulators of the chemical composition of the atmosphere. The claim is that, really, rain and photosynthesis are not particular functions but rather happen to be the effects of some more fundamental underlying physical or biochemical mechanisms.
3. "Millikan . . . and Neander . . . emphasize that the proper function of a trait, unlike its causal role function, plays a key role in determining whether the trait falls under biological categories like

1. The claims I am making here about the functions of the tongue in humans are clearly oversimplified. I am not saying that the tongue really only has one etiological function. This example is merely meant to serve illustrative purposes. I would like to thank an anonymous referee for pointing out that, strictly speaking, my example is not correct.

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'heart' and in determining what states of the trait count as dysfunctional" (Schwartz 1998, 211).

4. As mentioned in 3, etiological accounts supposedly allow us to adequately deal with malfunction or dysfunction. While on an etiological account, the ear of a hearing-impaired person still has the function to hear, one could, from Cummins's perspective, consider the nonfunctioning ear to no longer have a function because the ear fails to make any causal contribution toward hearing.

At this stage, one might be inclined to think that we should forget about systemic or causal-role functions and accept the etiological account of functions as the only appropriate treatment of biological functions. Things are, however, not this straightforward. There are several problems with the above-mentioned advantages of selected-effects accounts. Regarding point 1, we may say that, even though the introduction of natural selection into etiological accounts is helpful in certain ways, it is also considerably problematic. There is a wide range of literature trying to identify exactly in what way natural selection plays a role in selecting traits for their effects. I do not have the space here to go into any detail of these issues, but it will suffice for our present purpose to point to some of the most fundamental problems. Does natural selection have to be responsible for the initial fixation of a trait in order for the trait's selected effect to be functional? Or should it rather be maintained by natural selection to count as functional? Or do both conditions have to be satisfied? Do we have to look at a trait's distant past selection, recent past selection, or present selection? There is no consensus on these matters. Moreover, there is a whole range of practical problems as scientists often do not have sufficient empirical evidence to draw conclusions about when natural selection has been acting on a particular trait. Without such evidence, however, the ascription of proper functions becomes practically impossible. Another problem stems from the fact that the existence of a trait can never be fully explained in terms of its effects, unless only one particular trait would have the very effect at stake. The point is that usually one and the same effect can be brought about in different ways. Say that the effect at stake is spatial orientation. Now, this very effect can be achieved by means of either sight (e.g., in humans) or echolocation (as is the case in bats). Selection for an effect may explain the existence of a trait to some extent. But in the light of various possible traits producing the same effect, selection by itself can only give a limited explanation as to why a particular trait exists. Architectural constraints and the extent of genetic drift, for example, are likely to play a crucial role in explaining the existence of a particular trait.

Against point 2 above, one can argue that while there might be a threat

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of promiscuity in the Cummins context, etiological functions certainly are too restrictive. Hearing aids have not been favored by natural selection, yet they certainly have the function of making hearing possible. In this example, we have, of course, an intended design in the background that might be seen as a substitute for natural selection. One could, however, imagine a random mutation in an animal that leads to increased fitness. This mutation would seem to be functional even before natural selection acting on it. Similarly, a hearing device that was developed by accident, that is, without anyone's intention to build such a device, would still count as functioning as a hearing aid. Furthermore, Cummins has acknowledged that not every functional analysis based on his account will reveal anything particularly interesting. He says that "the appropriateness of this sort of explanatory strategy is a matter of degree, so is the appropriateness of function-ascribing statements" (1975, 765). How interesting, insightful, and nontrivial a functional analysis in terms of causal-role functions is will depend on the very system and its relationship to its functional parts. Being susceptible to functional gradation might, in fact, be counted as a virtue rather than a vice of Cummins's theory.

With respect to 3, it is worth pointing out that while Karen Neander contends that "biological categories must be defined by [selected-effects] functional analyses" (quoted in Amundson and Lauder 1998, 238), Amundson and Lauder argue that "causal role function in anatomy, if less philosophically fertile than selected-effect function, is on a much firmer epistemic footing. It also happens to be *ineliminably* involved in ongoing research programs. This alone ought to establish its credentials" (254). The point is that while selected-effects functions play their part in evolutionary biology, causal-role functions are indispensable in contexts such as anatomy or physiology. Selected-effects functional analysis does not and cannot provide the ultimate basis for biological categorization. Sterelny and Griffiths (1999) sum up neatly:

> We should not assume that biology traffics in only one type of function claim. Godfrey-Smith, Amundson, and Lauder all argue that there are two very different senses of function in biology. . . . Evolutionary biologists often use function in the sense defined by the etiological theory. Anatomists and physiologists, however, are not typically concerned with evolutionary history. They are interested in the activities an organism can perform: flying, digesting food, detecting viruses in its tissues, and the like. They explain how organisms perform these activities by functional analysis—by breaking down the overall task into parts that are performed by different parts of the organism. (223)

Millikan and Neander stress the importance of providing a functional

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account that is not based on commonsensical conceptual analysis but on actual scientific practice. Given that causal-role functions play a vital role in scientific disciplines such as anatomy and physiology, the motivations for adopting a pluralist stance become only too clear.[2]

There still remains the worry raised in point 4 above: how can a causal-role account accommodate malfunctions or dysfunctions? Perhaps, the most obvious and straightforward way of doing so is by means of reference to what an item's or trait's usual or normal function is. One might object that terms such as 'normal' or 'usual' are too imprecise to really help out. Yet, given the problems in determining the precise role of natural selection in accounting for a trait's proper function, the selected-effects account seems to fare no better.

5. Kitcher's Argument for Unity. We have seen how the antagonistic dialectic between etiological accounts and selected-effects accounts has developed to bear fruit in the form of an adoption of a pluralistic stance that sees both accounts as distinct. In this way, each approach has its own domain of proper application.[3] Kitcher not only acknowledges but in fact also welcomes this pluralism. Hence, he deplores that "philosophical discussions of function have tended to pit different analyses and different intuitions against one another without noting the pluralism inherent in biological practice" (1998, 277). Yet, somewhat at odds with the foregoing, he also tries to argue that there is some unity of conception that spans attributions of functions across the history of biology and across contemporary ascriptions in biological and nonbiological contexts. This unity is founded on the notion "that the function of an entity S is *what S is designed to do*" (258). Kitcher identifies two sources of design, intentions and natural selection, and he "claims that all biological attributions of function take place in a context characterized by design. But design can be relevant to attributions of function in more and less direct ways" (Godfrey-Smith 1998, 285). The distinction between direct and indirect demand satisfaction for functional ascriptions plays a central role in Kitcher's argument. He tries to bring out the distinction by means of providing an illustrative example along the following lines: we are meant to come up with a machine that is supposed to perform a particular task,

2. This is basically one of the key points, if not *the* key point, Amundson and Lauder attempt to make in their article (1998).

3. By saying that "each approach has its own domain of proper application," I do not mean that there are not many cases in which both approaches could be legitimately used. There are probably a considerable amount of cases in which both approaches identify the same traits/items to have the same function. I am making the weaker claim that one approach will be more adequate and fruitful than the other, depending on the nature of the scientific enterprise at hand.

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that is, the machine is going to have an intended function. Now that we are building our machine, a screw accidentally but serendipitously falls into a place where it makes a connection necessary for the machine to perform its intended function. According to Kitcher, "the screw has the function of making the connection" (1998, 260). Furthermore, he thinks this can be established because there is an indirect link to our intention for the machine to perform its particular task. "The function here is *grounded in the contribution* that is made towards the performance of the whole machine *and* in *the link between the performance and the explicit intentions* of the designer" (260; my italics). The causal-role function that is "grounded in the contribution that is made towards the performance of the whole machine" can be treated separately from the intended function of the machine. Yet, the "explicit intentions of the designer," in a way, predetermine what is functional and what is not. If it was not for the direct link to the intention of the designer of the machine, no causal-role analysis could be performed, for there would be no machine that was designed to perform its task. The causal role the screw plays would not count as functional if the designer had not decided what the machine was meant to do.

Having established the distinction between the direct and indirect ways in which design plays a role in the context of artifacts, Kitcher goes on to transpose his findings into the context of biology and natural selection. We have "the most general evolutionary pressures" (1998, 262) that determine what an entity "S is designed to do" (258). This context of design is, according to Kitcher, to be understood in terms of an environment-centered perspective, that is, the perspective on natural selection that holds "the principal features of the environment fixed [so that] we can ask what selective pressures are imposed on members of a group of organisms" (261). Once we know what selection pressures the environment determines, "we can specify more narrowly, recognizing needs to process certain types of food, to evade certain types of predators, to produce particular types of signals and so forth" (262). The particular mechanisms that allow an organism to tackle such tasks as processing a particular kind of food—for example, by means of either having the appropriate teeth or, alternatively, a suitable gastrointestinal system—can be best understood in performing a particular causal-role function. "There is a link to selection through the environment-centred perspective from which we generate the selection pressures that determine the functions of complex entities, and there is a mechanistic analysis of these complex entities that displays the ways in which the constituent parts contribute to total performance" (262). One may argue that really Kitcher's claim that "there is some unity of conception" is so weak that it is impossible to refute it, which would imply that niche-construction theory does not pose a threat to Kitcher's pro-

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posal. However, if we treat the unity claim in this way, one may wonder why one should even bother to establish some 'unity of conception'.

In this way, there is an analogue between the role played by the intentions of the machine designer and the environment-centered perspective of selection according to which the features of the environment are held fixed. Thus, whenever we perform a functional analysis, design (in the form of intentions or natural selection) always plays a role. The distinction is not to be drawn between cases in which design plays a role and in which it does not. Rather, the difference lies in whether intentions and natural selection play a direct role or whether they play a role in the background against which a functional Cummins style analysis is pursued. Thus, on this account, even in nonevolutionary scientific disciplines such as physiology "selection furnishes a context in which the overall design is considered, and, within that context, the physiologist tries to understand how the system works" (Kitcher 1998, 276).

6. Niche Construction and Its Implications for the Environment-Centered Perspective of Selection. Kitcher rests his argument on the premise that we adopt an environment-centered perspective of selection. This implies that "holding the principal features of the environment fixed, we can ask what selective pressures are imposed on members of a group of organisms" (1998, 261). This view is closely related to what Sterelny and Griffiths refer to as the classical notion of a niche. "Classic niches exist independently of their occupants; they constrain their occupants, and their occupants can vary in the degree to which they fit their niche. The environment drives adaptive evolution, and the niche identifies the aspects of the environment doing the driving" (1999, 225). Yet, this environment-centered view has been attacked and undermined by biologists advocating the evolutionarily consequential role of niche construction, perhaps most vehemently but also most compellingly by Odling-Smee, Laland, and Feldman (2003).

The ideas underlying niche-construction theory are, in effect, not entirely novel. They have been addressed, for example, by the biologist Richard Lewontin in the 1980s. In fact, Kitcher even mentions Lewontin's criticism of the environment-centered view, although he claims he can counter this criticism by saying that "the selection pressures on organisms arise only when we have held fixed important features of those organisms" (1998, 263). First of all, Kitcher seems to shift (rather than answer) the problem, by referring to "important features of those organisms." What, though, determines what is to count as important and what is not? Second, the point of niche construction is not that organisms are particularly malleable so as to adapt to their environments. Rather, the claim is that

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environments are malleable and thus can be changed by the organisms that inhabit them. The claim is that environments are not autonomous.

Niche-construction theory is based on the idea that while organisms are subject to selection pressures, they do in part, but to some evolutionarily relevant extent, modify these very selection pressures. "Evolutionary biology has provided a compelling explanation for why organisms appear so extraordinarily well suited to the environments in which they live: namely, through the action of natural selection, species have come to exhibit those characteristics that enable survival and reproduction. However, there are in fact two logically distinct routes to the evolving match between organisms and their environments: either the organism changes the environment, or the environment is changed to suit the organism" (Odling-Smee et al. 2003, 18).

There are an abundance of examples that illustrate how organisms, whether they are plants or animals, affect and modify their environments. Migratory birds pick their environment dependent on their foraging abilities, earthworms continuously alter the chemical composition of the soil they live in, and beavers build dams, thus constructing their own particular niche. Among other things, niche construction is likely to "transform selective environments to generate feedback that may have important evolutionary consequences" and "provide a second process capable of contributing to the dynamic adaptive match between organisms and environments" (Odling-Smee et al. 2003, 3). What is important here is that evolution on this account accommodates feedback between organisms and their environment; hence, niche-construction theory treats evolution as the result of a dynamic process, thus depicting evolution as a lot more complex than is commonly assumed. There is no such thing as an autonomous environment that can be seen to always dictate a particular context of background design.

Odling-Smee et al. demonstrate that "niche construction is extremely common" (2003, 6) Yet, in order for niche construction to be evolutionarily consequential, this will not suffice. What is required as well is that the modifications stemming from niche-constructing behavior or traits persist for a sufficiently long enough time and with enough local consistency. They point to two ways in which this persistence criterion can be satisfied:

a) "In each generation, *each individual repeatedly changes its own ontogenetic environment* in the same way" (9; my italics).
b) "All or a part of the consequences of one generation's niche-constructing activities persist in their modified form in the selective *environments of a succeeding generation*" (9–10; my italics).

With respect to a, Odling-Smee et al. provide the building of webs by

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spiders as an example. Interestingly, by building their webs, spiders seem to create a source of selection pressures acting on them for themselves (and probably other species as well). Thus, the building of dummy spiders in the web is likely to be a favored behavioral trait that allows the spider to fool birds that prey on them, hence, heightening their chances of not being eaten. The modification of the soil by earthworms mentioned above is a case that instantiates b. The soil, whose chemical composition has been radically altered over generations, has been passed on to the current generation in form of what Odling-Smee et al. call an 'ecological inheritance'. The earthworms inherit not only their parents' genes but also the selective environment that has been to a large extent determined by their ancestors. Given these and many further findings, Odling-Smee et al. conclude that "this capacity of organisms to modify some of their own selection pressures, whether between generations or within generations . . . requires us to revise the concept of adaptation in evolution and to adjust its meaning along the lines anticipated by Richard Lewontin" (2003, 16). Hence, it appears that we have a good reason to believe that Kitcher is not in a position to either neglect or overcome the concerns voiced by Lewontin as he does in his article. If his argument is meant to derive its strength from adopting the environment-centered perspective on selection, we seem to be forced to view this argument as unsupported.

One might object, though, that really niche construction is just an epiphenomenon of natural selection. Niche-constructing behaviors are nothing more than adaptations themselves. Against this criticism, Day, Laland, and Odling-Smee argue that "niche-constructing traits are more than just adaptations, because they play the additional role of modifying natural selection pressures, frequently in a directed manner, and in doing so they change the evolutionary dynamic" (2003, 82). Moreover, it is possible to turn this criticism on its head and ask whether natural selection is not merely derived from niche construction. In this way, the question regarding the relationship between natural selection (or adaptation) and niche construction is as insightful as asking who was there first, the chicken or the egg.

7. Possible Implications. I have tried to show, then, how Kitcher's commitment to the environment-centered perspective of selection is jeopardized by the role niche construction is likely to play in evolution. It seems, then, that we should commit ourselves to an uncompromised pluralistic view. In the light of the discussion of niche construction and its evolutionary implications, we may, though, wonder whether the correctness, or at least the adequacy and relevance of etiological accounts, might not be undermined. As touched on briefly above, there are a number of conceptual and practical problems pertaining to the analysis of proper func-

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tions. Now, the status of etiological functions seems to be even less clear if evolution rests on a dynamic process between natural selection and niche construction. It is not obvious to what extent a trait might count as having a proper function due to its being favored by natural selection for having a particular effect, if the organism to which this trait pertains is affected by its selective environment but also simultaneously affecting and modifying this very selective environment. As Griffiths says, "a feature will have a proper function only if it is an *adaptation* for that function. The trait must have been selected because it performs that function" (1993, 412).

Hence, not only Kitcher's argument for the conceptual unity of functions but also the viability of the selected-effects project appears to hinge to a large extent on the role that adaptation plays in the natural world. Gould and Lewontin had already highlighted the unwarranted overambitiousness of the empirical adaptationist program by pointing to the importance of architectural constraints. Suitably to the present discussion of functional analysis, they warn the reader that "one must not confuse the fact that a structure is used in some way . . . with the primary evolutionary reason for its existence and confirmation" (1979, 153). While it has been acknowledged, although often downplayed, that factors other than natural selection play a vital role in evolution, the recognition of the importance of niche construction may force us to reconsider the very nature of natural selection and, hence, also may force us to reconsider the role of etiological functional analysis. I am not in a position to say anything more conclusive about this in the present context. But if niche construction turned out to significantly modify our current notion of natural selection, pluralism with regard to functional analyses might be undermined after all.

8. Conclusion. In this article, I have provided an overview of the general developments in the literature on functional analysis. While earlier discussions were mainly concerned with the establishment of one 'true' account of functions, more recently there has been a trend toward a pluralistic stance that sees both etiological accounts and selected-effects accounts as legitimate approaches to functional analysis. Their adequacy depends on the specific scientific context. Kitcher's attempt to unify these two approaches via the notion of design fails in the light of recent developments in niche-construction theory. The latter undermines the premise of having a fixed environment functioning as an omnipresent source of design. Even though the role of niche construction for evolution has not yet been unequivocally determined, there is a whole battery of empirical and methodological evidence suggesting that niche construction is evolutionarily consequential. Both scientists such as Odling-Smee, Laland,

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and Feldman and philosophers such as Sterelny and Griffiths are supportive of or at least sympathetic toward the reconceptualization of the classical niche and, hence, the nature of natural selection.[4] Furthermore, I have touched on potential implications for etiological accounts stemming from such a reconceptualization of natural selection. Even though we may not be in a position to draw any decisive conclusions on that matter yet, the supporters of etiological accounts may have to worry about yet another complication affecting their account.

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4. See, e.g., Sterelny and Griffiths (1999), 272.

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