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NICHE CONSTRUCTION THEORY: DIFFICULTIES FOR A PRACTICE APPROACH TO THEORETICAL PLURALISM

by

CALEB HAZELWOOD

Under the Direction of Dan Weiskopf, PhD

ABSTRACT

In this thesis, I reconstruct C. Kenneth Waters' "practice-centered approach" to philosophy of biology. The objective of the approach is to resolve theoretical debates in biology by appealing to how theories are used to *predict* and *control* a phenomenon, not just *explain* it. By turning our attention to how theories are used in practice (e.g., developing new hypotheses or predicting novel results), we can see that two conceptually incompatible theories can actually coextend. I put the approach to the test with a contemporary case study: the debate between the Standard Evolutionary Theory and Niche Construction Theory. The debate centers on whether to amend the concept of an evolutionary process. Waters argues that the practice-centered approach resolves the debate with a pluralist framework. I argue that a pluralist framework is not warranted in this case, thus demonstrating that Waters' approach is not a panacea for all theoretical debates in biology.

INDEX WORDS: Metaphysics, Pluralism, Evolution, Niche construction, Theory, Practice

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CALEB HAZELWOOD

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1. INTRODUCTION

The "practice turn" in philosophy of biology can be understood as "a turn of our attention to scientific action" instead of theory alone; it "highlights the activities that are revealed when we look at the processes and doings of science by scientists and scientific communities (e.g., hypothesizing, testing, experimenting, theorizing, measuring) rather than exclusively on the products of science (e.g., knowledge, equations, theories)" (Kendig 2016).

The "practice versus theory" distinction has been reiterated many times over a lineage of intellectual ancestors (see Hacking 1983; Dupré 1995; Cartwright 1999; Ross et al. 2013; Ladyman & Ross 2007; Wimsatt 2007). Generally, the conversation is motivated by a worry that analysis in philosophy of biology relies too heavily on the explanatory role of theories. That is, philosophers of science frequently evaluate scientific theories based on how comprehensively they explain the relevant phenomena. Theories that are maximal in scope and unitary in their domain (e.g., theories that pick out biological universals) are preferred to theories that are more local and piecemeal in their application. For instance, evolutionary theory provides a universal explanation of the mechanism by which all biological species evolve (e.g., by natural selection). This is what I have in mind when I refer to the "explanatory role" of scientific theories in this paper. But if the goal of philosophical analysis of scientific knowledge is solely to understand how our theories *explain*, then it neglects the "practical role" of scientific theories—the ways in which a theory or concept is employed to guide scientific practice by establishing the criteria for new classifications or developing new hypotheses.¹

¹ In this paper, I'll use "theory" and "concept" interchangeably. I will not engage with the "concept" literature. For our purposes, a concept (e.g., "gene" or "species") will comprise a set of delimiting criteria that are employed to classify some phenomenon for some theoretical domain (e.g., genetics or ecology). In the following sections, I will discuss how we can evaluate those criteria based on their practical utility.

Scientific theories are multifaceted, and our philosophical analyses will be biased depending on which facets (viz., explanatory, practical, etc.) we choose to highlight. Ken Waters, for instance, calls for a "practice-centered" approach to philosophy of biology. A consequence of the "theory-focused" account (i.e., Waters' term for an approach that only highlights the explanatory role) is that it often invites universal interpretations of the core theories of a discipline, such as exception-less laws of nature. And while unveiling laws of nature may be a worthwhile pursuit in the harder sciences (like physics, for instance), expecting to find similarly fundamental features of the biological world is a dubious project (e.g., Beatty 1995). This is a problem for philosophy of biology, and Waters proposes a solution: philosophical analyses of biological theories ought to privilege their practical value over their explanatory value. However, the practical value of a theory is contingent upon the research context, as well as the empirical aims of the researchers. Consequently, competing theories may be more practically valuable in some contexts and not in others.

Waters' practice approach results in a theoretical pluralism that is *prima facie* appealing, and, in many case, compelling. However, he has (in my view) haphazardly presented it as a panacea for resolving the tension between *all* competing biological theories. In other words, Waters advertises the practice approach to pluralism as a "one size fits all" solution to theoretical debates in biology. In the following sections, I will reconstruct Ken Waters' account of a practice-centered approach to philosophy of biology. I will lay out how a practice approach can warrant theoretical pluralism about alternative theoretical frameworks. With provisional criteria for a practice approach to pluralism in hand, I'll apply them to an ongoing debate in evolutionary theory (viz., whether to extend the conceptual framework to include niche construction as an evolutionary process on par with natural selection). Waters (2010, 2014), as well as other

advocates of the practice approach (Love 2013, Uller and Helanterä 2018), argue that a practice approach can resolve the debate: we can be pluralists and embrace both frameworks depending on the relevant investigative contexts. I will argue, however, that the two conceptual evolutionary frameworks do not meet the criteria for a practice approach to theoretical pluralism because they are not differentially successful (i.e., one does not outcompete the other) in practical contexts. The upshot, I'll argue, is twofold: (1) contra Waters et al., the practice approach does not resolve the debate in evolutionary theory, and (2) the practice approach is therefore not a "one size fits all" solution to theoretical debates in the biological sciences.²

2. PRACTICE-CENTERED PHILOSOPHY OF BIOLOGY

In this paper, I refer to Waters' account (2010, 2014, 2017) when I talk about a "practicecentered" approach to philosophy of biology. But a bit should be said about the dichotomous characterization implied by Waters' shift of attention from "theory-focused" to "practicecentered" philosophy of biology. A turn to practice does not mean a rejection of theory *tout court*, but a rejection of theory divorced from biological practice. A turn to practice encourages an analysis of how theories play an integral role in experimentation, investigation, and manipulation. The thrust of the practice approach is in its recognition of the inextricable natures of theory and practice. So the shift of attention is not so much a shift away from theory *per se*, but a shift toward theory within its proper context: within the confines of investigative practice. In several places in the literature (2010, 2014), Waters clarifies the two approaches (viz., theoryfocused and practice-centered) by highlighting what kind of theorizing they enable. He warns

² Although Waters advocates for a pragmatic, localized, and piecemeal approach to scientific theories, his account does not entail antirealism. In fact, he has defended a realist interpretation of his view in (Waters 2017), and I have argued for a realist interpretation of a practice approach to philosophy of science in (Hazelwood 2018).

against one kind of theorizing in biology, which he calls "fundamental" theorizing, and advocates for the other, which he calls "toolbox" theorizing.

The former kind of biological theories, "fundamental" theories, often arise from focusing on how well a theory can, with maximum generality and scope, provide unified explanations of the relevant phenomena (though not necessarily, cf. Wimsatt 1976, 1980, 1987). When a biological theory is evaluated on its explanatory merits alone, it is often in virtue of being "guided by a commitment to find fundamental concepts and principles sufficient for providing a universal and unified account of nature" (Waters 2010). For example, philosophers of science have traditionally expected that the discipline of physics reveals what is fundamental to the world, meaning in this context that physics reveals features of the world that are common to everything, everywhere, and all of the time (Waters 2017). A similar pattern of analysis in philosophy of biology delivers similar results. Philosophers of biology often expect that our best theories of the living world will reveal fundamental categories like species, fundamental evolutionary processes like natural selection, and fundamental boundaries of "individuals" like genes or organisms. In other words, one expects that our best theories of the living world will reveal categories, processes, and boundaries that are common to everything in the living world, everywhere in the living world, and all of the time in the living world. Recall that this is a problem for Waters because, on his view, pursuing the "fundamental concepts and principles" of biology is futile. Waters is an epistemological pluralist: he believes that we can carve up the world in numerous incompatible yet noncompeting ways depending on the relevant empirical questions we aim to answer. On the other hand, divorcing a theory from its relevant practice (by evaluating it strictly in terms of the scope and generalizability of its explanatory power) often

commits one to a doctrine of epistemological monism, viz., there is *one correct way* to carve up the world (Love 2013).³

The latter kind of biological theories, "toolbox" theories, often arise from a turn of attention to scientific practice. Waters borrows the metaphor from William Wimsatt (2007) and Nancy Cartwright (1999, et al. 1995). Wimsatt's slogan for toolbox theorizing says it in a nutshell: "In our flight from a monolithic and exceptionless logic of science we should not miss the many techniques that are wide but not universal in scope—a 'toolbox of science'" (Wimsatt 2007). Waters puts it another way:

...the aim of scientific theorizing is to construct causal models that explain aspects of the processes in the domain and that provide a basis for manipulation [of] those processes. Achieving this aim entails articulating a multiplicity of theoretical concepts and causal principles that can be drawn upon to construct models that might decompose the causes of some processes in a multiplicity of ways. In such cases, some concepts and models offer the best account of some aspects of the given process, others provide the best account of other aspects. (2010)

Toolbox in hand, Cartwright, Wimsatt, and Waters advocate for a kind of theoretical pluralism. Waters in particular says that for any given phenomenon, a multiplicity of theoretical "tools" (e.g., concepts or causal principles) will be necessary for constructing successful accounts of the phenomenon. The world is messy, and not so easily divided up among universal principles and processes. So messy, in fact, that Waters believes theoretical explanation of it ought to be pragmatic. Waters spells out his use of pragmatism nicely in a paper on biological individuality and the practices of individuating in (2018). His explanation can be reformatted for our purposes here: "instead of asking 'what is an [x]?' as if there is an essence to (or a paradigm of) [x],

³ Fundamentalism about successful scientific theories assumes they provide the single best account to explain the relevant phenomena. Considers Waters' description of the position in (2014): "[Scientific theorizing] entails articulating the fundamental theoretical concepts and causal principles that can provide a basis for constructing models that decompose the causes of each and every process in the uniquely correct way. Proponents of this view stress the idea that there is, of course, just one way the world actually is, and the aim of theorizing is to describe, in a principled manner, the one way it actually is."

philosophers should examine how biologists individuate [x] and ask what purposes these individuating practices can serve."

These two kinds of theorizing, fundamentalist and toolbox, are intended to highlight the aforementioned roles of a scientific theory: the *explanatory* and the *practical*, respectively. But a bit more must be said about these roles before we proceed. I do not wish to characterize the dual facets of a scientific theory as if they are mutually exclusive. On the contrary, the explanatory success of a theory is closely linked to its capacity for spurring prediction, control, and manipulation of the relevant phenomena (see, for instance, Hempel 1991, 2002, and Woodward 2003). Therefore, any theory that is successful from a practical (read: pragmatic) standpoint will also be successful from an explanatory standpoint, given that our practical success is in light of some deeper knowledge about the relevant phenomena. But here's the catch: the explanatory success of a theory is constrained by the limitations of its practical context. A theory will only successfully explain what falls within the domain of its predictive power. Particular species concepts, for instance, will only successfully explain the relevant phenomena that they are employed to classify. The same goes for concepts that demarcate genes, and, as we'll see in §5-6, evolutionary processes. The point in teasing these roles apart is to demonstrate that, from the perspective of a practice approach, explanations that are not rooted in practical (viz., predictive, manipulative, etc.) success risk purporting to reveal some universal, biological absolutes that fall outside of the jurisdiction of the relevant research context.

In §3, I will demonstrate how Waters' practice approach can be applied "in practice." I will provide an example of a practice approach to pluralism, viz. pluralism about multiple species concepts. On Waters' account, different species concepts can act as different tools in our theoretical toolbox. However, as I'll argue in §5 (contra Waters), the same principle does not

apply to a contemporary debate in evolutionary theory, viz. whether we ought to expand the conceptual framework and privilege niche construction as an evolutionary process on par with natural selection. According to the practice approach, two competing evolutionary theories—the Standard Evolutionary Theory and Niche Construction Theory—compete along different practical axes and demonstrate differential success. They rely on two alternative concepts that are employed to demarcate "evolutionary processes" (i.e., processes that are causally privileged in the evolution of a population). I object to this conclusion on the grounds that the evolutionary process concepts do not differ in practical value—only in explanatory scope. The debate is disanalogous to the species example in important ways, as I explain below. Therefore, the solution to the debate falls outside the jurisdiction of Waters' practice approach.

3. THE PRACTICE APPROACH "IN PRACTICE"

Thus far, I've reconstructed Waters' practice-centered approach to philosophy of biology, and juxtaposed it with a theory-focused approach. I have distinguished the kinds of theorizing that are involved in each approach (viz., toolbox theorizing and fundamental theorizing, respectively). I have furthermore explained that Waters' practice-centered approach privileges the practical role of a theory (viz., how it is employed in specific research contexts to draw classifications, develop hypotheses, spur new lines of inquiry, etc.) over its explanatory role (viz., how it is generalized to elucidate the relevant phenomena). A brief example will help to distinguish these roles. Consider two alternative species concepts: the biological species concept and the phylo-phenetic species concept. The biological species concept (BSC hereafter) demonstrates practical value: it provides a clear rubric for drawing boundaries around animal species, viz., around populations of reproductively isolated and interbreeding organisms. But the BSC cannot represent the sole theoretical criteria for species membership because it is incapable of explaining the nature of asexual prokaryotic species. Bacterial species, for example, are not reproductively isolated because they do not interbreed. Moreover, mechanisms such as lateral gene transfer regularly blur the genetic lines between one bacterial lineage and another. For the microbiologist in the lab or field, the BSC is too restrictive. Therefore, microbiologists employ an alternative species concept: a phylo-phenetic species concept (PPSC hereafter). The PPSC also demonstrates practical value: it provides a clear rubric for drawing boundaries around microbial species, viz., around populations marked by a conventional threshold of genetic and morphological similarity.

Here, we see the two roles of the concept on display. The species concept can be operationalized in different ways (e.g., with a specific mechanism for reproductive isolation, with thresholds of similarity, etc.). We do not invoke concepts in a theory simply so we can provide an explanation for the phenomena. We invoke concepts in a theory (e.g., the species concept in ecological theory) because they help us *in practice*. In other words, pluralism about the species concept did not come about on the grounds that one concept did not sufficiently explain all of the relevant phenomena. It came about because one species concept (the BSC) was practically unavailing in an ecological sub-discipline—microbiology—that comprises the vast majority of life on earth. A plurality of species concepts is *necessary* to accommodate all of relevant phenomena that fall within the investigative domain of the discipline.

With this example in mind, we can begin to see how its advocates build a bridge from the practice turn to theoretical pluralism: in the presence of two theoretical perspectives, we can accept both as legitimate formulations of the concept. Why? Each enables researchers within a sub-discipline to advance the practice of the sub-discipline, and each is preferred to the other in a particular practice. If I am a mammalogist studying mammal species, I'll rely on the BSC. If I

am a microbiologist studying bacterial species, I'll rely on a phylo-phenetic species concept. Each concept is a tool in the theoretical toolbox, and each one is appropriate given its investigative context. Just as you wouldn't take a Phillips screwdriver to flathead screw, you wouldn't use the BSC to demarcate bacterial species. This is not to say the Phillips screw is any less a screw than the flathead, and the same holds for species concepts. Therefore, we can take them together. Simply put, we acknowledge both formulations of the species concept—that is, we can be pluralists about the species concept—because each concept allows practitioners to successfully carve up a particular subset of the relevant population. Each concept has jurisdiction over some particular subset where it is most successful. Thus, with a set of delimiting criteria in place, practitioners are able to classify species, evaluate borderline cases, observe patterns about the species, develop hypotheses, and make inferences about future species phenomena that fall under the domain of the relevant species concept.

At this juncture, the critic might object that the practice approach grants *too much* authority to the pragmatic aims of practitioners. Does it follow from the practice approach that we ought to be pluralists about *all* theoretical tools used by practitioners? Does it beget an "anything goes" approach to scientific theories? If some scientist uses some theory in some investigative context, are we to immediately legitimize that theory and take it seriously? In other words, to return to our example, are we to recognize the BSC and the phylo-phenetic species concept *just because* they are both used by practitioners?⁴

⁴ We find a response in Wimsatt (2007): "Traditional relativists have tried to recognize truths in different perspectives while in effect assuming they are each complete and competing. They then seem inexorably pushed into saying that if these can *each* be right, then (in a sense) *nothing*'s right, and (therefore) *anything* goes. But if we see this as the problem of how to integrate complementary partial-truths, then the demands on reality are strong and multifaceted, but not impossible. Accepting a common referent becomes an essential tool in seeing how to reconcile and integrate the different views."

Surely this is not what advocates of the practice approach mean to say. In fact, we can identify criteria for a practice approach to theoretical pluralism in the literature (Ereshefsky and Reydon 2015, Uller and Helanterä 2018). I contend that a practice approach will justify pluralism about two (or more) theories when one is better suited to advance the relevant scientific practice than the alternative(s). This is a loaded claim that requires some unpacking. What does it mean to be "better suited" to advance the relevant scientific practice than the other theoretical contenders? It is an integral criterion in various instantiations of the practice approach. For instance, Alan Love says, "the proliferation of idealized theory structures is in the service of fine-grained empirical inquiry. Their existence, maintenance, and longevity are governed by fecundity. This fecundity is most observable within disciplinary specialties" (Love 2013). Other advocates of the practice approach put forward similar criteria. In fact, some philosophically minded biologists even maintain that, when considering alternative theoretical perspectives, "their constructive evaluation should be on the basis of their ability to stimulate new questions and predict patterns and phenomena that would otherwise appear surprising" (Uller and Helanterä 2018). Likewise, they say, "Those arguing for more substantial conceptual change must strive towards showing that [the alternative theory leads] to a more theoretically and empirically progressive research programme" (ibid.).

The Lakatosian undertones should not be lost on the reader. In fact, other practicecentered advocates have argued explicitly for a Lakatosian approach to alternative theoretical frameworks. Consider Ereshefsky and Reydon in (2015):

To obtain such a criterion we turn to Lakatos' (1970) distinction between progressive and degenerating research programs. For Lakatos, a progressive research program must be both theoretically and empirically progressive. It is theoretically progressive if it predicts novel facts—facts not predicted by other theories. It is empirically progressive if those predictions are corroborated. A research program is degenerative if it fails one of those requirements: that is, it fails to generate novel predictions or the predictions it generates

remain unconfirmed. An important aspect of Lakatos' schema is that the progressiveness of a research program is comparative. The issue is not whether a research program is progressive simpliciter, but whether it is more progressive than its rivals.

In a Lakatosian framework, a research program is supposed to be rejected when shown to be degenerative compared to alternatives. However, the practice approach makes a contribution to the Lakatosian research program: the role of *context*. A theoretical framework can be both progressive when compared to alternatives and degenerative when compared to alternatives; it depends on the investigative context in which the framework is employed. For instance, the BSC is going to be a progressive concept in some investigative contexts (e.g., mammalogy) and degenerative in others (e.g., bacteriology). Each is theoretically progressive relative to the other in its appropriate context because each predicts facts (i.e., each draws species boundaries) that the other cannot. Say, for instance, you—an ecologist—happen upon an undiscovered animal population in the field that exhibits behavioral and morphological similarities. If you want to determine how many species were present in that population, you will need the BSC, and not the PPSC, to predict the number. In fact, a conceptual barrier divides the two formulations of the concept such that the language of the BSC doesn't even translate to the sub-discipline of microbiology, and vice versa. Therefore, the BSC will predict novel facts by elucidating species boundaries that the PPSC is incapable of predicting.⁵

The practice approach allows for theoretical frameworks to be progressive in some domains of inquiry and degenerative in others because, depending on the "disciplinary specialty," one theoretical framework may be "fecund" where another may not be. It may "stimulate new questions and predict patterns and phenomena that would otherwise appear surprising;" it may predict "novel facts—facts not predicted by other theories." Simply put, I

⁵ It should be noted that a concept is not a prediction tool *per se*, and I don't mean to give that impression. Instead, a concept is central to the theory, and the theory may be employed to predict.

argue that the practice approach advocates for theoretical pluralism about *progressive* theoretical frameworks. That is, a theory may be endorsed when there is a practical, investigative context in which it is progressive (i.e., when it spurs the generation and interpretation of novel empirical content) relative to competing theories. If *multiple* theoretical frameworks pass muster in different practical contexts, the net result is pluralism.

Now that we are equipped with a provisional criterion for a practice approach to theoretical pluralism, we can apply the approach to theoretical debates over rival conceptual frameworks. In this paper, I am interested specifically in whether the practice approach can help to solve the current debate about "evolutionary processes" in evolutionary biology, viz., whether to maintain or amend the mainstream conceptual framework. In order to apply this approach, we must first say a bit about the debate, and then reconstruct some practice-centered solutions advanced in the literature.

4. THE EXTENDED EVOLUTIONARY SYNTHESIS

The Standard Evolutionary Theory (SET) is the dominant contemporary framework in evolutionary biology. It represents the synthesis of multiple theoretical domains of biology such as Darwinian natural selection, Mendelian genetics, and molecular genetics. Its advocates explain evolution through processes of random variation, inheritance, and selection, implicating these processes in a causal account of evolution. According to the SET, populations evolve over time due to particular processes that act on them—i.e., evolution occurs in virtue of natural selection, genetic drift, migration, and mutation (Scott-Phillips et al. 2014). These processes are causal primarily because they affect allele frequencies and the concentrations of variations of genetic (and, consequently, phenotypic) traits. Evolutionary phenomena that do not directly affect the dynamics of gene pools, e.g., developmental phenomena such as niche construction or developmental plasticity, are not recognized in the SET to possess the same causal primacy as processes that directly affect the dynamics of gene pools. Developmental processes may cause evolutionary processes, but they don't cause a change in a population's DNA sequence frequency.

Meanwhile, advocates of an extended evolutionary synthesis (EES) paint a different picture. Advocates hold that theorists have long (and erroneously) neglected developmental phenomena such as niche construction and developmental plasticity when building a causal account of evolution. They argue that the SET requires an overhaul: in light of accumulating evidence, we ought to amend our evolutionary theory such that it accounts for developmental phenomena as evolutionary processes instead of only those phenomena that directly affect the dynamics of population gene pools (e.g., natural selection, migration, drift, etc.). Because developmental processes generate raw materials for natural selection (e.g., novel epigenetic programs, novel pathways of heredity such as cultural, behavioral, ecological, epigenetic, or microbial inheritance), we ought to view developmental and evolutionary processes as inextricably intertwined, with each feeding into the other.

This debate, viz., whether to amend our evolutionary theory to incorporate developmental phenomena as causal processes of evolution, provides an example of "one place where issues of theory boundaries, content representation, and a diversity of model applications are on display" (Love 2013). In other words, there is a disagreement about which theory evolutionary biologists ought to embrace. Should we stand by the contemporary evolutionary theory that has dominated much of the past century, the SET, or should we adjust how evolutionary theory is taught, represented, and used in practice through an extended synthesis? Should we couch new evidence in our current framework, or should we expand the framework to account for new evidence such

that it tells a different causal story? If the distinction seems trivial, practitioners assure us it is not. Alan Love reports that the "wrangling over centrality [of causal processes in evolutionary theory] is not mere rhetoric. It represents genuine differences" (Love 2013). Kevin Laland says likewise, "This is no storm in the academic tearoom. It is a struggle for the very soul of the discipline" (Laland et al. 2014).

One such point of contention is the role of niche construction in evolution. Niche construction is "the process whereby organisms actively modify their own and each other's evolutionary niches" (Laland et al. 2016). Paradigmatic examples include beavers building their dams, hermit crabs inheriting their shells, bobtail squid "seeding" their habitats with symbiotic microbes, etc. (ibid., Godfrey-Smith 2012). According to advocates of an EES, an injustice is done to evolutionary theory by continuing to ignore the causal primacy of niche construction. By modifying its own environment, so the story goes, a population plays an active role in how it evolves. Niche construction can relieve or place novel selection pressures on a population. According to some practitioners, this alteration of selection dynamics shows that populations do not passively and blindly evolve in response to environmental pressures, but that the fit between organism and environment is the product of intention and design.

Advocates of the EES are building models with this revamped causal story in mind. Instead of only privileging the processes that directly influence gene frequencies as evolutionary processes, they seek models that place niche construction as an evolutionary process on par with natural selection. In fact, advocates are so convinced by the causal story of this unsung evolutionary hero that they have introduced a new theory of evolutionary causation: Niche Construction Theory (NCT).

However, not all practitioners agree that NCT is a necessary addition to the evolutionary synthesis. For example, Gregory Wray and Hopi Hoekstra, among others, insist that, "The evolutionary phenomena championed by Laland and colleagues are already well integrated into evolutionary biology, where they have long provided useful insights" (Wray et al. 2014). These practitioners, whom I'll call advocates of the SET, point back to Darwin's final monograph, *The* Formation of Vegetable Mould, through the Actions of Worms, With Observations on their *Habits* (1881), to demonstrate that even the father of natural selection was thinking about the feedback between organism and environment before the SET was synthesized. The difference for advocates of the SET is that they see the contemporary synthesis as being comprehensively capable of incorporating, explaining, and motivating further research into niche construction. It does not warrant a new theory; its role in evolution is already accommodated by the SET. Put another way, advocates of the SET recognize that niche construction occurs—this is indisputable. They also recognize that modifying one's environment affects selection dynamics by relieving some pressures or placing new pressures on a population. However, they differ in the extent to which they acknowledge the *causal* influence of niche construction. One can hold that niche construction occurs while simultaneously holding that evolution reflects changes in gene frequencies that result from altered selection dynamics. Practitioners who build theoretical models of selection dynamics need not account for niche construction as an evolutionary process, because the effects of niche construction are indirectly seen in the changes in gene frequencies. On the other hand, niche construction theorists claim that such models miss the point. While it is true that the effects of niche construction are ultimately seen through changes in gene frequencies, models that neglect niche construction as an evolutionary process fail to acknowledge the environment and the organism as participants in a coevolving system—a

dynamical feedback loop. According to advocates of NCT, natural selection alone is insufficient to accommodate the downstream effects of habitat modification. In the following section, I put these two competing narratives in the context of an example (viz., the evolution of lactose tolerance) to illustrate the conceptual tension.

5. PUTTING THE APPROACH TO THE TEST

It seems obvious *prima facie* how a practice approach à la Waters would propose to resolve this debate: we should shift our attention from an abstract theory toward the practices of evolutionary biology. Any efforts to determine a single, comprehensive evolutionary theory are liable to invite notions of fundamental evolutionary processes. That is, by playing referee between the SET and NCT and looking for one to win out over the other, we run the risk of making theoretically monistic assumptions (i.e., expecting one theory to account for all evolutionary processes in all living systems, everywhere, all of the time. Recall that Waters does not believe such biological absolutes exist. As such, no such concept of evolutionary processes can be elucidated, because evolutionary processes are defined on *pragmatic* grounds). On the other hand, if we were to apply a practice approach to the debate by shifting our attention to theories within investigative contexts of the discipline, we would recognize that it serves practitioners to employ the SET in some cases while it serves them to employ NCT in others.

The approach is supposed to usher in a sort of theoretical armistice; it encourages us to recognize the contextual advantages of each theory. It expects this conclusion will be extended beyond debates about concepts like "gene" or "species" and can even offer a solution for theoretical frameworks like evolutionary theory. Indeed, Waters clearly suggests that a practice approach could come to the rescue in evolutionary biology, given the field's historical fixation on finding the single best theoretical framework:

Although philosophers now disagree about whether the fundamental theory is (or should be) a theory of population genetics, evolutionary genetics based on Price's equation, or a theory that fuses evolution and development, many [e.g., Wray et al. 2014] remain passionately committed to the ideal that there must be one best way to understand evolution, one right way of parsing the causes that divides evolutionary processes into distinct and non-overlapping kinds. (2014)

His response on behalf of a practice approach should help us anticipate how it might aim to

resolve the debate between the SET and NCT:

Why should we believe evolutionary processes must fall neatly into distinctive kinds of processes, that each of these kinds of processes can be fully represented by one model-type, and that the collection of model-types explaining the different kinds of processes can be subsumed under a single set of fundamental principles? If evolutionary processes do not fall into distinctive kinds, then theorizing as if they did, might be counterproductive in the same way as insisting upon a single rigid concept of [the] gene would be counter-productive in genetics. (ibid.)

Consider, for example, a question introduced above: is niche construction an evolutionary (as opposed to a strictly developmental) process? According to a practice approach, if, when scientists build models to account for selection dynamics in a given system, and those models are built to meet different, perhaps incompatible aims, it should sometimes make sense to answer "yes" to this question, and at other times it should make sense to answer "no." In other words, Waters et al. would likely encourage us to recognize components of the SET and NCT as tools in our theoretical toolbox, such that modeling niche construction as an evolutionary process will be appropriate in some cases and inappropriate in others.

There is vocal support for this in the literature. As previously mentioned, there are biologically minded philosophers and philosophically minded biologists who have rallied behind the practice approach to theoretical pluralism as a solution to the debate in evolutionary theory. In a recent article, evolutionary biologists Tobias Uller and Heikki Helanterä "attempt to shed some light on the nature of the fault line" that divides interpretive understandings of niche construction (2018). The authors seek to reconcile the two conceptual frameworks by doing away with the Popperian notion that one theory ought to give rise to the other (i.e., that one is falsified by anomalous data). Science does not progress through falsification, they insist, but through alternative Lakatosian research programs. These theories aren't directly competing. Instead, the authors suggest, we can use a practice approach to warrant theoretical pluralism about the two conceptual frameworks. Therefore, we ought to embrace NCT as an alternative research program and take its conceptual contribution together with the conceptual contributions of the mainstream evolutionary theory. We can take these together, the authors suggest, because building our models based on one conceptual framework versus the other will make sense in particular research contexts. This is fundamental for scientific progress:

At least some biologists who argue that niche construction should motivate conceptual change in evolutionary theory explicitly identify development of multiple, co-existing, conceptual frameworks as an important task for scientists...We suggest that the niche construction controversies should be understood as attempts to develop alternative research programmes, not in response to anomalous data, but motivated by a belief that the scope, structure, and content of the dominant research programme is too limited. (ibid.)

The authors echo Alan Love's position that this dispute is not mere rhetoric; they argue that, "contrary to how some, perhaps most, evolutionary biologists interpret the situation...the disagreement is not primarily due to a perceived lack of attention to niche construction phenomena. Instead, the debate reflects that biologists hold a variety of views on causation in evolving systems" (ibid.).

But this last line anticipates my objection to the practice approach's claim to resolving the theoretical debate in evolutionary theory. Uller's and Helanterä's analysis of the rift between theoretical frameworks is thorough, empirically grounded, and an excellent resource for understanding how niche construction is incorporated on both sides of the debate. However, their conclusion (viz., that we ought to embrace the standard view of niche construction and NCT as "multiple, co-existing, conceptual frameworks") seems unwarranted given an analysis of the indistinguishable practical (i.e., predictive) success of each theory.

Recall that my reconstruction of a practice approach to theoretical pluralism holds that such an approach will allow multiple theoretical frameworks that are progressive relative to each other to co-exist. However, they must be progressive with respect to different investigative aims. The differential in their practical success must be measured along multiple axes (e.g., predicting new facts, developing new hypotheses, corroborating hypotheses, etc.), and each must be progressive relative to the other on at least one axis in order for us to take them together. In other words, within the various research contexts of a discipline, theory A may be much better suited to address the aims of some practitioners, whereas theory B may be better suited for other practitioners. Meanwhile, the practitioners are asking questions, investigating patterns, and making predictions that are better accommodated by one theoretical framework over another. Therefore, we can be pluralistic about which is the "right" theory.

If Uller and Helanterä are correct, and we ought to embrace NCT as a legitimate, coexisting conceptual framework, it ought to be in virtue of the fact that NCT contributes something to the research that the SET cannot, and vice versa. Each must be progressive relative to the other with respect to a particular investigative aim in order for us to justify taking them both together as legitimate, co-existing conceptual frameworks. The authors put it plainly:

If we consider the niche construction perspectives as attempts to formulate alternative research programmes, their constructive evaluation should be on the basis of their ability to stimulate new questions and predict patterns and phenomena that would otherwise appear surprising; not on the basis of the perceived explanatory sufficiency of the majority view of evolutionary theory. (2018)

On Uller's and Helanterä's account, we ought to be able to demonstrate that the niche construction perspective stimulates new questions and predicts new patterns or phenomena. In

other words, we ought to be able to demonstrate that, at least for *some* legitimate domains of inquiry, NCT is a progressive conceptual framework.

Therefore, the burden of proof is on the advocate of the practice approach: they must demonstrate that, as a progressive conceptual framework, NCT stimulates new questions, predicts new patterns, or identifies novel facts. Let's assume that Uller and Helanterä are correct in asserting that NCT *does* expand the empirical content of evolutionary biology. We must now decide whether a progressive conceptual framework must necessarily be the source of new questions and predictions, or whether it may do so by mere contingency. I will defend the former interpretation: in order to compete along different axes, progressive frameworks are progressive by necessity.

By "progressive by necessity," I mean that one framework expands the empirical content of a discipline by operationalizing a concept that is *in principle* incompatible with other useful explanatory concepts in the discipline. On the other hand, a framework that contingently expands the empirical content of a discipline does so by operationalizing an explanatory concept that is *not* in principle incompatible with other useful explanatory concepts. A contingently successful explanatory concept will rely on other explanatory concepts to stimulate new questions, predict new patterns, or identify novel phenomena. There is no conceptual barrier that divides the two frameworks or renders them explanatorily incompatible. In fact, a contingently successful concept may even be reducible to other concepts against which it alleges to compete. And because these multiple concepts are compatible and perhaps even interchangeable at certain points, we cannot say their success is measured along different axes. It will just be the case that the contingently successful concept is equally successful as its competitor, because both concepts will be capable of generating the same insights, hypotheses, patterns, etc. A necessarily successful concept, meanwhile, will expand the empirical content of a discipline in a way that its competitor cannot. This is because the lines of inquiry it inspires, as well as the patterns it predicts, will be conceptually incompatible with those of any other useful concept in the discipline.

It will be useful to revisit an earlier example: species concepts. Recall that a conceptual barrier divides our alternative species concepts (viz., the biological species concept and a phylophenetic species concept) to the extent that the application of one concept makes predictions that the other *could not make*—not even in principle. The BSC's particular mechanism of speciation (viz., reproductive isolation) is operationally useless for the research aims of microbiologists, whose organisms of interest do not sexually reproduce. Thus, according to a practice approach, theoretical pluralism about these two concepts is warranted and entailed by a conceptual barrier that prevents the application of any one concept in *all* investigative contexts. The predictions, patterns, and phenomena recognized by the BSC could not be recognized by the microbiologist's phylo-phenetic species concept. In other words, these species concepts compete on multiple axes. Those axes are picking out microbial species and picking out animal species. Each species concept is more successful (and therefore progressive) relative to the other along one of those axes. Thus, a flavor of theoretical pluralism that embraces both of these species concepts is grounded in the non-overlapping domain of phenomena that they are employed to investigate.

But this is not analogous to our example in evolutionary theory. The niche construction perspective does not make any predictions that could not be made *in principle* by the standard evolutionary framework. In a paper coauthored by skeptics and an advocate (viz. Kevin Laland), the authors state that, "currently these two accounts differ more in terms of their style of *explanation* than dissimilarities in *empirical findings or predictions* (Scott-Phillips et al. 2014,

my emphasis). They provide a case study to illustrate this point: the positive correlation between the frequency of alleles for lactose tolerance in a population and a history of dairy farming in the community. The consensus hypothesis for quite some time—the hypothesis formerly endorsed by the mainstream SET—was that an established persistence of the alleles for lactose tolerance preceded the agricultural practice of dairy farming. As more members of a population began to exhibit tolerance to lactose, it made better sense to shift toward a dairy centered farming practice. NCT provides an alternative hypothesis, and one that relies on gene-culture coevolution. In this alternative hypothesis, it is the agricultural practice that preceded the persistence of alleles for lactose tolerance in a community. By modifying their habitat (viz. through reorienting their agricultural practices around milk cows), these ancestral populations constructed their own selective niche. They manipulated their selective environment in such a way that members of the population with the proper alleles for lactose tolerance would, given the new available resources, fare far better than those who lacked the proper alleles. As a result, lactose tolerant members of the population would be more fit in this new environment (i.e., they would be more reproductively successful), thus leading to the persistence of the alleles in the population. So, the advocate claims, the niche construction perspective generates novel insights and predictions in a way that the SET does not, leading to "the recognition of dynamical feedback between the cultural practice and the allele for lactose persistence (i.e., the selective environment and genetic trait are coevolving)" (ibid). One causal arrow in that dynamic system between environment and organism is natural selection; the other, according to the advocates of NCT, is niche construction. Because both arrows are necessary in this dynamic system—here's the leap—niche construction is an evolutionary process on par with natural selection.

An advocate for the practice approach may look at this and, at first glance, be quite satisfied. It appears to fall well within the practice approach's jurisdiction. After all, we have two accounts: SET (which says a, b, c, and d are evolutionary processes) and NCT (which says a, b, c, d, and e are evolutionary processes). With respect to the standard model of a passive, blind, abiotic selective environment, the SET will do just fine. The classic example is the white moth flying across the forest floor versus the gray moth flying across the forest floor; you don't need niche construction to tell you which phenotype will persist in the population. Along such axes (i.e., when investigating the evolutionary histories of populations who have evolved in static circumstances), the SET is clearly progressive relative to NCT. However, with respect to models of dynamic systems of feedback between environments and populations, NCT will outcompete the SET. Why? Because it allows us to operationalize a concept where the selective backdrop is not passive and blind. Instead, it constantly evolves in tandem with, and as a result of, the population whose evolution it facilitates. Framing niche construction as an evolutionary process in this way will generate novel predictions, just as it has done in the case of lactose tolerance. If, according to the practice approach, the proof is in the pudding, then NCT has demonstrated its utility by expanding the empirical content of the discipline. Therefore, we can be pluralists about the two theories. Furthermore, it is a pluralism grounded in the operational value of those theories in practice.

Here's the rub: while it is true that NCT has expanded the empirical content of evolutionary biology by introducing a novel hypothesis, and while it is true that the NCT hypothesis (environment preceding trait) has replaced the SET hypothesis (trait preceding environment), the success of NCT in this case is *contingent* upon its shift in focus from a passive environment to a dynamic environment. However, there is nothing about framing niche construction as an evolutionary process (as opposed to a developmental phenomenon) that is *necessary* in order to reach this hypothesis. There is no conceptual barrier between the SET and NCT that would prevent them from arriving at the same predictions. This is because "the newly established facts remain explicable within [the standard] paradigm... What would be necessary to justify the major claims made for NCT [viz., that niche construction is an evolutionary process in its own right] would be for it to make a forward prediction of something that would *not* be explicable within the standard theory" (ibid.) As we can see from the advocate's own explanation (viz., "dairy farming causes a change in the *selective environment* to favor the lactose absorption alleles"), a story about the evolution of an adaptation from a niche construction perspective ultimately breaks down to a story about natural selection (ibid., my emphasis). In other words, the case for one evolutionary process relies on its reduction to another evolutionary process. Therefore, there is nothing that is *per se* incompatible about these two formulations of the concept. They overlap substantially, and, with respect to practical success, neither outcompetes the other, as they are both equipped to make identical predictions.

We can contrast this with other paradigmatic cases of concept pluralism. The phylophenetic species concept better serves the aims of the microbiologist while the biological species concept better serves the aims of the mammalogist (Ereshefsky 1998). One species concept is progressive relative to the other on one particular axis, and vice versa, so we take both species concepts together. Likewise, the classical gene concept better serves the aims of the population geneticist while the molecular gene concept better serves the aims of the molecular geneticist (Waters 2014). One gene concept is progressive relative to the other on one particular axis, and vice versa, so we take both gene concepts together.

The reason we can say these homonymous concepts are progressive relative to one another on separate axes is because they are divided by conceptual barriers that restrict their application to non-overlapping investigative domains. One species concept will not reduce down to another, nor will it require conceptual furniture from the other in order to be operationalized in practice. The same holds for the two gene concepts previously mentioned. However, the same will not be said of the concept in question, viz. evolutionary processes as instantiated by the SET or NCT. There is no conceptual barrier that restricts their application to non-overlapping investigative domains. SET and NCT can accommodate the same phenomena and arrive at the same predictions. The primary difference is that one will do so while explaining niche construction in terms of evolutionary processes, and the other will do so by explaining it in terms of developmental processes. No matter your preferred flavor, *both* perspectives will tell a story about the evolution of an adaptation, and the explanatory heavy lifting will be done by natural selection. While the use of NCT may motivate the expansion of empirical content from practice, there is nothing about its competitor that bars it from generating the exact same insights. Thus, from the standpoint of a practice approach, both NCT and the SET perform equally. Where they differ is solely along an *explanatory* axis, and that falls outside of the jurisdiction of a practice approach to theoretical pluralism.

6. CONCLUSION

If my analysis is correct, it follows that the practice approach to philosophy of biology does not warrant theoretical pluralism as a solution to the debate about Niche Construction Theory and its status as a privileged evolutionary process. A practice approach aims by definition to shift attention away from the explanatory value of a theory toward its practical value. When two concepts (or theoretical propositions) are identical in operational value and differ only in explanatory value, then a practice-centered analysis is ineffective in resolving the debate. We will resolve the debate about niche construction by continuing a dialogue about what it means to be an evolutionary process. Is it necessary that an evolutionary process be a process that directly affects the frequency of alleles in a population? Can we expand our account of evolutionary causation such that niche construction gains pride of place alongside natural selection? This is the thrust of the debate: "whether niche construction and natural selection are of equivalent explanatory importance" (Scott-Phillips et al. 2014). The resolution of the debate is beyond the scope of this paper. Fortunately for my argument, however, it is also beyond the scope of a practice approach to theoretical pluralism.

Advocates of a practice approach—specifically the ones targeted in this paper—present it as if it's a "one size fits all" solution to theoretical debates in the biological sciences. In several places, they explicitly advertise it as providing the solution to several debates in evolutionary theory, including the debate about NCT. However, once we identify the rubric for theoretical pluralism (as I have extracted it from the Lakatosian frameworks of Uller & Helanterä 2018 and Ereshefsky & Reydon 2015), and we follow the logic of the approach to its conclusion, we find that the approach does not deliver as advertised. As it turns out, some theories simply compete along one axis: explanatory value. SET and NCT are two such theories. The upshot is that the practice approach, while very useful for fragmented concepts such as "species" or "genes," does not offer a "one size fits all" solution to theoretical debates in the biological sciences.

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