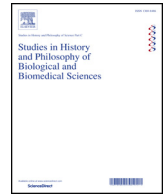




Contents lists available at ScienceDirect

Studies in History and Philosophy of Biol & Biomed Sci

journal homepage: www.elsevier.com/locate/shpsc

Synthesising arguments and the extended evolutionary synthesis

Andrew Buskell

Department of History and Philosophy of Science, Free School Lane, University of Cambridge, Cambridge, CB2 3RH, UK

A B S T R A C T

Synthesising arguments motivate changes to the conceptual tools, theoretical structure, and evaluatory framework employed in a given scientific domain. Recently, a broad coalition of researchers has put forward a synthesising argument in favour of an Extended Evolutionary Synthesis ('EES'). Often this synthesising argument is evaluated using a *virtue-based* approach, which construes the EES as a wholesale alternative to prevailing practice. Here I argue this virtue-based approach is not fit for purpose. Taking the central concept of niche construction as a case study, I show that an *agenda-based* approach better captures the pragmatic and epistemological goals of the EES synthesising argument and diagnoses areas of empirical disagreement with prevailing practice.

1. Introduction

Does evolutionary theory need 'expanding' or 'extending'? Recently, a number of researchers have answered in the affirmative. Diagnosing deficits in what they label 'standard', 'traditional', 'Neo-Darwinian', or frequently, 'Modern Synthesis' evolutionary theory, these researchers argue for a different approach to evolutionary theory. These *synthesising arguments* are attempts at bringing about a broad reorganisation of the concepts, methods, explanatory standards, and structure of evolutionary research.¹

The component parts of these synthesising arguments—novel concepts, methods, causal machinery, and evaluative standards—are objects of continuing philosophical attention.² Here, however, I focus on how synthesising arguments *in general* are taken to motivate alternate theoretical frameworks. I do so by examining Kevin Laland and colleagues' 'Extended Evolutionary Synthesis' (hereafter; 'EES'). Their synthesising argument holds that prevailing evolutionary research obscures important evolutionary phenomena; notably the plastic nature of organismic development, non-genetic sources of inheritance, and the active role of organisms in modifying evolutionary trajectories. Highlighting the causal complexity of evolutionary processes through work in evolutionary developmental biology, parental effects, and niche construction, EES proponents argue for a radically updated evolutionary theory.

My aim is to outline how synthesising arguments, like the one made by EES proponents, should be evaluated. As I show in more detail below, EES proponents and sceptics frequently apply a *virtue-based* approach. This takes synthesising arguments to motivate full-scale

alternatives to prevailing practice—distinct packages of concepts, models, theoretical assumptions and explanatory standards. So understood, the respective merits of synthesising arguments can be compared to prevailing practice by contrasting the extent to which each displays theoretical virtues. Yet I will argue that this virtue-based approach is unsuited to evaluating the EES synthesising argument insofar as it obscures the pragmatic, empirical, and epistemological reasoning that motivates proponents. I argue instead for an agenda-based strategy. This evaluates synthesising arguments on the basis of their ability to mobilise empirically apt machinery in the pursuit of structured research agendas (Brigandt & Love, 2010; Love, 2010). Using the debate around niche construction as a case study, I show how adoption of the agenda-based approach provides a more illuminating evaluatory framework for the EES synthesising argument.

2. Challenging standard evolutionary theory

Developed across multiple publications and drawing on expertise from a number of empirical and philosophical literatures, the EES synthesising argument is a highly visible attempt at challenging the consensus practice of researchers in evolutionary biology (Kitcher, 1993; Buskell, 2019). And while many authors support the EES (e.g. Jablonka & Lamb, 2005; Müller, 2007; Müller & Pigliucci, 2010; Pigliucci, 2007, 2009), their views differ in both subtle and substantial ways. Here I focus on the collaborative papers and volumes associated with Kevin Laland and colleagues, who have been vocal champions of the EES (e.g. Laland, Kim, Odling-Smee, Hoppitt, & Uller, 2011; 2013a, b, 2014, 2015, 2017; Laland, 2015, 2017, 2018; Uller and Helanterä

E-mail address: ab2086@cam.ac.uk.

¹ For instance, Raff (1996); Amundson (2005); Carroll (2005, 2008); Müller (2007); Pigliucci (2007, 2009); Müller and Pigliucci (2010).

² See, for instance; analyses of purportedly novel evolutionary concepts (Müller, 2007; Pigliucci, 2008); the causal claims made in evolutionary explanations (Laland and Sterelny 2006; Walsh, 2015); the structure of evolutionary theory (Brigandt & Love, 2010; Love, 2010), and the nature of theoretical change in evolutionary theory (Love, 2013, 2017).

<https://doi.org/10.1016/j.shpsc.2019.101244>

Received 30 July 2018; Received in revised form 18 December 2019; Accepted 27 December 2019

1369-8486/ © 2019 Elsevier Ltd. All rights reserved.

2018). When I speak of the EES, I thus have Laland's version in mind.

The EES synthesising argument—and any synthesising argument more generally—is contentious because it challenges longstanding theoretical assumptions, research practices, and textbook presentations in evolutionary research. It is thus unsurprising to find critical responses to the theoretical (Charlesworth and Charlesworth 2017; Gardner, 2013; Wray et al., 2014), methodological (Buskell, 2019), and conceptual proposals of the EES (Scott-Philips et al., 2011; Dickins & Rahman, 2012; Gupta, Prasad, Dey, Joshi, & Vidya, 2017a, b). In the two following subsections, I sketch both the EES objections to consensus practice, and what successor concepts and concerns they think should take centre stage in evolutionary research. Following this, I turn in the next section to analyse how disputes over the merits of the EES should be evaluated.

2.1. Gene-centrism and fractionation

While many recent synthesising arguments object to a prevailing focus on adaptive function—suggesting that more attention is needed to organismic form³—the primary objections voiced in the EES synthesising argument are to *gene-centrism* and *fractionation*. Gene-centrism holds that variation in phenotypes are ultimately attributable to variation in genes; that genes hold a privileged role in explaining phenotypes (Oyama, 2000). Fractionation, by contrast, maintains that the “component processes of evolution—inheritance, development, adaptive change, and the introduction of novelties—are distinct and autonomous.” (Walsh, 2015, xi) For EES proponents, these two assumptions act to entrench consensus practice and obscure the visibility of issues around developmental bias, developmental plasticity, inclusive inheritance, and niche construction (Laland et al., 2015; Uller and Helanterä, 2019).

EES proponents thus display a ‘particular discontent’ towards behavioural ecological and population genetic models where gene-centrism and fractionation are prominent assumptions.⁴ These models have a tendency to treat evolutionary processes as discrete, sequential, non-interacting processes. Alan Grafen's famous articulation of the ‘phenotypic gambit’ is a case in point:

“The phenotypic gambit is to examine the evolutionary basis of a character as if the very simplest genetic system controlled it: as if there were a haploid locus at which each distinct strategy was represented by a distinct allele, as if the pay-off rule gave the number of offspring for each allele, and as if enough mutation occurred to allow each strategy the opportunity to invade” (Grafen, 1991, p. 6).

Grafen's gambit is barefaced in its gene-centrism: genes represent phenotypes. More than this, Grafen's gambit separates out processes of inheritance, development, adaptive change, and the introduction of variation: inheritance is genetically based, development is the translation of these genes into phenotypes, adaptive change is the result of natural selection operating on these expressed phenotypes, and variation is introduced by an ample supply of mutations.

In section four (‘Comparing and Evaluating the EES’) I flesh out in

³ Rudolf Raff (1996, xvi) argues that “biologists need to understand and incorporate the underlying rules of developing systems into a more comprehensive theory of evolution.”, Sean Carroll (2000, 280) that “Evo Devo constitutes the third major act in a continuing evolutionary synthesis.”, and Robert L Carroll (2000, 30) that “The present generation of evolutionary biologists [...] has the opportunity to integrate [evolutionary developmental biology] into a new synthesis, to guide evolutionary research and teaching in the next century.” Love (2017) calls these *developmental form challenges* insofar as they challenge standard evolutionary theory by putting forward synthesising arguments that boost the visibility of issues around the origin of evolutionary novelties, deep genetic homology, and the developmental production of organismic form.

⁴ The phrase ‘particular discontent’ is from Welch (2017).

further detail how and why the EES argues against fractionation and gene-centrism. To foreshadow those arguments here, proponents argue that genotypes underdetermine phenotypic outcomes, and that the plasticity of development, combined with the ability of organisms to change their selective environments, delegitimises ideas around genetic control and the separability of evolutionary processes (Scholl & Pigliucci, 2015; Laland et al., 2015. Cf. Welch, 2017, p. 272). But I continue in the next subsection by outlining the positive pitch for the EES—one where the complexities of developmental plasticity, non-genetic sources of inheritance, and organismic agency are taken to play an important role in both the dynamics and direction of evolutionary change.

2.2. The EES synthesising argument

Articulating the EES synthesising argument is difficult. Like other synthesising arguments, proponents of the EES do not put forward theoretical axioms, exceptionless empirical generalisations, or canonical sets of models.⁵ And when EES proponents do appeal to models and theoretical constructs, it is not always clear what roles these are to play—for instance, whether these form a cohesive ‘core’ around which an expanded evolutionary theory can be based, or a looser, eclectic network of empirical models, assumptions, and case studies (Lewens, 2015; Love, 2017; Fábregas-Tejeda & Vergara-Silva, 2018). Reconstructing the EES synthesising argument is further complicated by the fact that its most explicit theoretical reflections to date are found in qualitative statements and pictorial representations (e.g. Laland, Odling-Smee, Hoppitt, & Uller, 2013a, 2014, 2015, 2017; Laland, 2015; Müller 2007). This should not be taken as an indictment. Like all scientific endeavours—including the consensus practice it aims at replacing—the EES is a work in progress. Nonetheless, the predominantly qualitative and pictorial presentation of theory structure does present exegetical difficulties.

As a first pass, the EES synthesising argument can be approached by developing the *defining themes* of the EES (paraphrasing Laland et al., [2015]):

1. **Constructive Development:** development is plastic, responding to exogenous and endogenous causes in systematic ways that can shape evolutionary trajectories.
2. **Reciprocal Causation:** organisms and their environments mutually influence one another. As a result, organismic activity can be both a cause and consequence of evolutionary change.

While these themes are inspired by empirical work, they are not theoretical statements, do not straightforwardly function as guidelines for empirical research, and are not unambiguous guides to the structure of a reorganised evolutionary theory (Fábregas-Tejeda & Vergara-Silva, 2018; Love, 2010, 2017). Instead, these themes provide framing for scientific work; an epistemic narrative that can link together disparate postulates, practical recommendations, and guiding assumptions. In other words, they are a guide with which “to think about, and interpret, new and familiar problems in evolutionary biology” (Laland et al., 2015, p. 6). The narrative aims at replacing the prevailing assumptions of fractionation and gene-centrism with a picture of evolutionary change where “the developing organism cannot be reduced to separable components, one of which (e.g. the genome) exerts exclusive control over the other (e.g. the phenotype).” (Laland et al., 2015, p. 6) On this revised view, organisms are taken to be in constant contact and negotiation with their environment in ways that affect their downstream viability and fitness.

Within this narrative, the EES mobilises six core assumptions which

⁵ See, for instance, Alan Love's (2013, 2017) reconstruction of Sean Carroll's (2005, 2008) synthesising argument.

offer more concrete guidelines for scientific practice (Laland et al., 2015). These foreground the complexity of evolutionary causation and highlight phenomena lacking visibility in consensus practice. Yet it is worth stressing that these too are not unambiguous, and require substantial interpretation to guide research. These six assumptions are that: (i) organisms and environments are linked by pervasive mutual causal influence, (ii) there are non-genetic sources of heritable variation, (iii) the structure of organisms bias the production of heritable variation, (iv) plasticity in development can facilitate substantial changes in phenotype, (v) developmental plasticity allows for flexible and dynamic accommodation to change over both developmental and phylogenetic timeframes, and (vi) these features scale-up to explain macroevolutionary events.

Below I develop three examples to show how these assumptions might be put to work in explaining evolutionary phenomena. The first of these is drawn from work of EES proponents. The second and third are drawn from without, but exemplify work amenable to the framework.

The first example comes from the work of Daniel Schwab, Casasa, and Moczek (2017) on heritable non-genetic transmission in dung beetles (genus *Onthophagus*). Dung beetle mothers craft faecal brood balls where they lay their eggs. Larvae grow up in these brood balls, which they consume through their early development. Eggs are laid on maternal faecal pellets—somewhat gloriously referred to as a ‘pedestal’—which are consumed by the growing larvae. As Schwab and colleagues have shown, these pedestals serve as a reliable transmitter of symbiotic gut microflora. Removal of the pedestal, or substitution with a pedestal from a sister species, leads to delayed development and reduced growth. Yet these deleterious effects can be counteracted by feeding larvae experimentally cultured pedestals (Parker, Dury, & Moczek, 2019; Schwab, Riggs, Newton, & Moczek, 2016).

The effects of this non-genetic transmission extend into the larval environment. In the process of moving about and consuming the brood ball, larvae defecate. In so doing, they distribute their symbiotic microflora throughout the brood ball. This microflora then acts as an ‘extended stomach’, breaking down the plant and fungal biomass composing the bulk of the brood ball. As compared to normal larvae, those that were regularly moved to sterilised brood balls had delayed development, atypical morphologies, slower growth, and smaller overall body size. Importantly, females given this sterilisation treatment produced fewer offspring and made smaller brood balls. The spreading of faecal matter by *Onthophagus* larvae is thus an instance of both non-genetic transmission and niche construction; everyday movement and excretion of waste inoculates of the brood ball with helpful microbial communities, creating a more salubrious developmental environment.

Second, consider the turtle carapace. The carapace (the dorsal component of the shell) is an evolutionary novelty, produced in development by the fan-shaped spreading of ribs that later fuse with vertebrae and form hardened dermal plates. Because the carapace is formed of the ribs, turtle scapulae (shoulder blades) are forced to develop *inside* the ribcage of the animal—a unique feature among animals. As Kuratani, Kuraku, and Nagashima (2011, 3) write, this feature “appears to have broken the basic rules of the vertebrate body plan”, as there are no intermediary steps between the shoulder blades being outside and then inside the ribcage. In other words, a coordinated suite of changes is needed to explain how functional scapulae were suddenly brought within the ribcage. The disjunctive nature of this morphology has led several authors to suggest that the carapace is a saltation, brought about by sudden changes to cell migration during embryonic development (Rieppel, 2001; Robert, 2004).

Yet the current leading explanation of the evolution of turtle carapace suggests that far more mundane changes are at work. According to Kuritani and colleagues (2011), selection increasingly pushed scapulae towards the head of the turtle to accommodate the spreading of the ribcage. Eventually, this continued selection forced a change; pushed against the outer barriers of growth, the cellular progenitors of

scapulae were *folded inside* the developing ribs.

The folding account helps explain some puzzling developmental features of turtles, notably, the positioning of the supporting musculature. Deep muscles connecting the shoulder to the trunk form simultaneously with the formation of the scapulae. These end up inverted as compared to other vertebrates—a feature that can be parsimoniously explained by embryonic folding. The supporting superficial muscles develop later in embryo formation, connecting to bones in their inverted placement (Nagashima et al., 2009). Thus, the plasticity of developmental processes not only explains the placement of turtle scapulae inside the ribcage, but also the connection of musculature supporting such a radically altered vertebrate morphology.

Third, consider the barnacle *Chthamalus anisopoma*, which cements itself on rocky intertidal areas on the northern shores of the Gulf of California. The typical morph of *C. anisopoma* is ‘conical’, and has a volcano-shaped shell with the aperture of the barnacle at the top of the cone, parallel to the rock to which it is attached. The atypical morph is ‘bent’, and grows so that the mouth is perpendicular to the attached rocks (Lively and Curtis, 1986c). The bent morph incurs a number of costs associated with its shape including slower growth and lower fitness—so why does it occur?

As Lively and Curtis (1986a, b) argues, the bent morph seems to be induced by the presence of the carnivorous snail *Acanthina angelica*. *A. angelica* uses a spine on its shell to prise open barnacle apertures—but is decidedly less effective at preying on the bent morphs. Interestingly, it is only in the higher tidal areas where *A. angelica* predate that one finds the bent morphs. This suggests that the presence of the snail induces morphological change in the barnacle. Though the underlying pathway responsible for the change is currently unclear (Mokady, Mizrahi-Perl-Treves, & Achituv, 2000), sensitivity to the presence of predators during development likely explains the two strikingly different morphologies.

These examples differentially illustrate the core assumptions and defining themes of the EES. They emphasise non-genetic inheritance, variable rates of change, developmental plasticity, mutual webs of causal interaction, and the role of organismic activity. Together they exemplify the causally complex phenomena that EES proponents believe to be underappreciated and undertheorized by consensus evolutionary practice. And while some of these phenomena can plausibly be explained by standard approaches to life history theory and signalling theory, EES proponents argue that such consensus research methods will fail to adequately capture the underlying causal processes. Again, this is because such methods are taken to buy into gene-centrism and/or fractionation.

As proponents see it, the most effective case for the EES synthesising argument is its ability to integrate and explain the complex realities of biological causation and change at multiple levels. Such complex and multi-scale causation implicates the assumptions of gene-centrism and fractionation as obfuscatory. If organisms are in continual negotiation with the world, creating complex webs of mutual influence—perhaps generating non-genetic regularities that ‘flip’ latent developmental switches—then the autonomy of evolutionary processes and the privileged character of genes may be undermined. Emphasising the research areas of developmental bias, developmental plasticity, niche construction and inclusive inheritance, the EES synthesising argument is an attempt to reorient researchers so that such complex webs of mutual influence come into view.

3. Evaluating Synthesising Arguments

3.1. The virtue-based approach

EES proponents are adamant that their framework marks a departure from “‘business as usual’ science: it requires conceptual change.” (Laland et al., 2015, p. 10) As they see it, the concepts they put forward “are neither part of nor implied by the Modern Synthesis.” (Pigliucci, 2008, p. 75). And these are important to boot; these

“additional evolutionary processes [...] are more than just non-essential ‘add-ons’ and may be as important in shaping evolution as those recognized within the field over the past century.” (Laland et al., 2015, p. 10) How are we to evaluate these claims, and determine whether evolutionary research should indeed be revised and reorganised?

In many places, opponents and sceptics adopt a *virtue-based* strategy to evaluate the EES. This takes synthesising arguments to put forward alternative and comprehensive packages of concepts, theories, and empirical standards, whose merits can be evaluated using theoretical virtues. This strategy adopts language and tools from the large literature on theory change. As is well-known, Kuhn (1970, 1977) argued that when in a position of choice, scientists evaluate alternate paradigms on the basis of their virtues, with Kuhn identifying predictive accuracy, consistency, unification, scope, simplicity, and fecundity as important candidate virtues (1977, 321–322). Similar accounts that combine an analysis of theoretical structure together with a model of theory choice can be found in Lakatos’ (1978) notion of ‘progressive research programmes’, Laudan’s (1977) ‘research traditions’, and Kitcher’s (1981, 1989) derivational account of understanding and unification.

My focus here is on articulating the strategy by which one should evaluate the EES synthesising argument. And while my argument touches upon philosophical debates about theory change, nothing in what follows hinges on the underlying structure of those theories. What is important is that on the virtue-based approach, researchers evaluate synthesising arguments as comprehensive alternatives to consensus practice—whether one takes this alternative to consist in collections of canonical models, sets of laws, or exceptionless generalisations.

Language identifying the EES as a comprehensive alternative to standard evolutionary practice is widespread. Pigliucci (2007), for instance, adopts Kuhnian terminology, suggesting that the EES represents the latest development of the modern synthesis paradigm. Laland et al. (2015) also uses Kuhnian language, noting that the “EES requires no ‘revolution,’” (10) emphasising continuity with previous evolutionary theory while simultaneously highlighting the distinctive conceptual resources of the EES. More conservatively, Scott-Phillips, Thomas, E Dickins, and West (2011) dismiss the EES by arguing that standard evolutionary theory is sufficient for the “routine progress of science” (39) and is able to deal with anomalous results as they pop up. Elsewhere, Uller and Helanterä (2019) and Laland (2018) invoke Lakatosian research programs as part of an argument for the EES: the EES represents a progressive problem shift, one that can encompass a greater amount of empirical content. Pievani (2012) comes to a similar conclusion, also within a Lakatosian framework.

This framing—that distinguishes the EES as an alternative package of methods, theories, and concepts—is especially conspicuous in the language EES proponents use to justify *why* the EES is required. As they see it, the EES targets the ‘core’ of consensus practice, whether this is articulated in terms of ‘core assumptions’ (Laland et al., 2015), ‘central tenets’ (Pigliucci and Müller 2010), or ‘core logic’ (Müller 2007). Laland et al. (2015) for instance contrast what they call “classical [Modern Synthesis] core assumptions” (2) with those of the EES. It is the repudiation and replacement of this ‘core’ set of ideas that legitimises the EES as a full-scale alternative. It also motivates EES proponents to generate a set of predictions which can be directly contrasted with those aissuing from standard evolutionary theory; with the comparison meant to emphasise the broader scope, application, and empirical fruitfulness of the EES.

The virtue-based approach is embedded in these analyses. Distinguishing the EES and standard consensus practice as alternative theoretical packages, researchers then propose which theoretical virtues should be most important when deciding between them. EES proponents are often motivated by the belief that “the scope, structure, and content of the dominant research programme is too limited.” (Uller and Helanterä, 2019) As a result, they identify a range of desiderata they think an improved evolutionary theory should have. It should, for

instance, have “predictive power” and provide a deep “understanding of the mechanisms of evolution” (Laland et al., 2015, p. 11). More than this, an improved evolutionary theory would maximise empirical content (Uller and Helanterä, 2019) and be expansive enough to “accommodate the insights of developmentally minded evolutionists” (Laland et al., 2013, p. 733).

These are all sensible desiderata. Yet they are poor measures for comparing and evaluating the EES with standard evolutionary theory.

Consider that Kuhn himself argued that theoretical virtues are vaguely defined and “readily prove to conflict with one another,” (1977, 322). This is a point that has recently been made more explicit. Linking the literature on theory-choice to Arrow’s impossibility theorem, Okasha (2011) shows that under certain assumptions, evaluating theories on the basis of theoretical virtues leads to situations where no theory emerges as preferable.⁶ This account draws attention to the idealisations and simplifications made in models of theory-choice. Two I want to draw attention to here are the way that this literature assumes that theories can be fully articulated in propositional form, and that researchers have epistemic closure over these propositions—that the entailments of propositions are known. Kitcher’s (1981, 1989) account of unification is a case in point. This account provides principles for evaluating different sets of propositionally articulated theoretical statements (‘general argument patterns’) on the assumption that one knows the set of conclusion that could be derived from such statements.⁷

I suspect that a kind of ‘product-oriented’ stance—one that understands theories as completed packages of theoretical statements—motivates the epistemological assumptions around propositional articulation and closure, and gives them more weight than they deserve when evaluating theories. When theories are understood as completed products, it makes sense to evaluate them in virtue of their ability to generate of epistemic goods or exemplify virtues. But when theories are dynamic and in the process of being articulated, this product-oriented stance misses all the action. In such situations, theoretical virtues mislead as to the pragmatic reasons motivating different theoretical structures, and obfuscate the existence of distinct research objectives.

Such a product-oriented stance is noticeable when EES proponents frame their objections as a response to the Modern Synthesis. Historians of science have been sceptical both that there is such a thing as ‘standard’ or ‘modern synthesis’ evolutionary theory, that this represents a consensus in early twentieth-century evolutionary biology, and that such a consensus continues to structure contemporary evolutionary research. While it is certainly the case that there was impressive theoretical work undertaken in the first half of the twentieth century, these historians argue that there was no definitive theoretical package that spread through all of the life sciences. The current perception of a unified theoretical construct called the ‘modern synthesis’ reflects a historical achievement; a united front that combined multiple attempts at constructing unity (Smocovitis, 1996) through political and social organisation (Cain, 1993; Milam, 2010). Seeing evolutionary theory as operating under a shared synthetic framework may even be harmful, insofar as it misleads as to the diversity of empirical and theoretical work in the life sciences, and obscures broad scientific trends (Cain, 2009; Depew & Weber, 1996; Love, 2010).

My aim here is not to deny the usefulness of a virtue-based approach wholesale. Such an approach allows for a degree of generality and formalisation that can facilitate modelling of scientific processes, the

⁶ The key assumptions that Okasha interrogates are that theories are evaluable by ordinal and incommensurate global measures: that preference rankings contain no information about the intensity of preferences, nor that there is a standard currency for comparing these preferences.

⁷ Similar comments apply, *mutatis mutandis* to Sober’s (1975) early account of simplicity—though this account targets *hypotheses* rather than theory simplicity.

formulation of evaluative principles, and articulations of theoretical structure. Nor do I claim that the analyses here are original: I am restating old complaints that the virtue-based or ‘top-down’ perspective obscures the pragmatic reasoning involved in arbitrating epistemic and theoretical disputes on the ground. And Kuhn himself famously voiced scepticism that measurements of theoretical virtues “could be unambiguously stated” and that “an appropriate weight function is at hand for their joint application.” (1977, 326)

Yet I think these complaints are worth restating, since they show the weaknesses of the virtue-based approach. Researchers do not have closure over their concepts: philosophers of biology continue to argue over central concepts such as natural selection (Lewens, 2010), fitness (Rosenberg & Bouchard, 2015) and perhaps even evolution (Tanghe, De Tiège, Pauwels, Blancke, & Braeckman, 2018). Even purportedly novel concepts neither ‘part of nor implied by the Modern Synthesis’ can be construed in gene-centric and fractionated ways (Lynch, 2007; Welch, 2017). Moreover, it is difficult to definitively nail down the theoretical resources of both the EES and standard evolutionary theory so as to measure their theoretical virtues. And to the extent that a virtue-based evaluative strategy relies on global metrics, it is unlikely to capture the ground-level reasons that could actually adjudicate between these competing accounts. All of this suggests that the virtue-based approach is ill-suited to evaluate the EES synthesising argument.

3.2. The agenda-based approach

The solution, as I see it, is to reject the virtue-based strategy and opt for what I’ll call an agenda-based approach. This articulates the pragmatic and epistemological benefits of evolutionary frameworks by looking to scientific practice. On this agenda-based approach, the implications of different theoretical frameworks are evaluated on their own merits by examining how the methods and concepts they employ satisfy an organized assemblage of research aims—what Brigandt and Love (2010) have elsewhere called *problem agendas*.

Problem agendas are “a list of things that need to be addressed or multiple, interrelated questions, which have grown up over time” (Brigandt & Love, 2010, p. 422) within a scientific domain. The relationships between these research aims may be complex, mixing empirical and theoretical needs, with questions and sub-questions embedded in hierarchical ways. Moreover, problem agendas are historical and value-laden, reflecting the social, political, and epistemological impulses of numerous researchers over time.

I engaged in some rudimentary agenda-based work in the sections above, articulating the kinds of research questions motivating EES proponents: by rejecting gene-centrism and fractionation, the EES targets questions around the role of extra-genetic inheritance, the nature and efficacy of developmental bias, exploratory processes, and phenotypic plasticity (Müller 2007).⁸ And below, I will zoom in to focus on a particular set of research questions concerning niche construction. There I’ll argue that while not all EES research aims conflict with those of standard evolutionary theory, some do. These latter represent places where fruitful debate between consensus practice and the EES can occur. Unsurprisingly, these are areas where complex causation in development jars with the more simplified and sequential models based around gene-centrism and fractionation.

A useful way of thinking about the interrelationship among problem agendas within a single domain is to take them as distinct theory presentations (Griesemer, 1984; Love, 2013, 2017). Theory presentations are selective idealisations of underlying theoretical content; sets of concepts and inferences mobilized in the service heterogeneous

research aims.⁹ Developing an analogy from Griesemer (1984), we can think of these presentations as akin to different maps of the same terrain: each map provides a distinct perspective on an area, highlighting some features while ignoring others, and will have different uses and users as a result. Maps charting the distribution of avians might be of interest to birders and conservationists, while a map of resource deposits in the same area will interest others. In the same way, theory presentations selectively highlight concepts and inferences in order to navigate the epistemic terrain in the pursuit of distinct sets of research questions.

What EES researchers suggest is that under a range of circumstances, the assumptions of gene-centrism and fractionation are not helpful in navigating the epistemic terrain of evolutionary phenomena—they are not empirically apt for pursuing a wide range of research aims.

Empirical aptness is a relationship between a researcher’s conceptual and inferential resources and the generation of epistemic goods (e.g. explanations, models, further articulation of theory, revised concepts). Because problem agendas are targeted at heterogeneous research aims, standards for evaluating how such goods are produced will be similarly heterogeneous—often local and tied to progress on specific empirical projects. Indeed, it is often through empirical investigation itself that “assumptions about what it means to generate an adequate explanatory framework” (Brigandt & Love, 2010, p. 96) are revealed. Through empirical investigation, research questions can be refined, explanatory standards better articulated, and conceptual tools tweaked.

Let me step back for a moment and reflect on the assembled pieces of machinery. The EES puts forward a synthesising argument; an attempt to reorganize the concepts, methods, explanatory standards, and theory of evolutionary theory. As I have suggested, proponents and opponents alike have tended to apply a virtue-based approach to evaluate this argument. This takes the synthesising argument to represent a comprehensive alternative, one whose merits are evaluable by measuring and comparing its theoretical virtues to those of consensus practice. For reasons stated above, I think this approach is not particularly illuminating. The agenda-based approach I motivate in its place suggests that the EES synthesising argument is better evaluated as a set of research objectives, one that mobilises the theoretical content of evolutionary biology in a novel way. Evaluation of synthesising arguments, on this approach, consists in determining the extent to which the EES is able to articulate these objectives, mobilise conceptual tools, and generate epistemic goods in the pursuit of specific research aims. In the remainder of the paper, I will demonstrate and argue for the merits of the agenda-based approach. As I will show, it is a better lens through which to view synthesising arguments: the agenda-based approach allows for more accurate reconstructions of the argumentation, pragmatic goals, and position of proponents; furnishes a better framework for evaluation, and lastly; provides a means for diagnosing areas of real disagreement.

One important corollary of the agenda-based approach is the extent to which it can help resolve some of the contradictory rhetoric of EES proponents. In particular, it can help to reconcile claims that boost the radical importance of proposed reforms with those that emphasise continuity and overlap with standard evolutionary theory. Laland and colleagues often suggest that the EES requires conceptual change—it is not ‘business as usual’ evolutionary theory. Yet they also deny the need for radical change, suggesting that “all processes central to contemporary evolutionary theory [...] and its empirical findings, remain important” (Laland et al., 2015, p. 10). The two seemingly contrary positions can be reconciled by understanding the EES as motivating a

⁸ I note that while Müller does discuss problem agendas, this is used to characterise the structure of standard evolutionary theory. He does not advocate an erotetic strategy either for reconstructing the structure of evolutionary theory or evaluating its merits.

⁹ As Love (2013) argues, the idealization involved in constructing theory presentations is akin to idealization in scientific models; complex phenomena are represented in simplified ways to highlight particular evidential and epistemic linkages.

different problem agenda. The research aims pursued by the EES may require novel conceptual tools—yet this does not require a rejection of those employed in consensus practice, which may be used to pursue a very different set of research aims.

Along similar lines, the agenda-based strategy can also help to rationalise the ‘particular discontent’ that proponents of synthesising arguments have towards prominent adaptationist and optimization-based assumptions in standard presentations of evolutionary theory. One risk of such standard presentations is that they may embody assumptions so entrenched so as to be invisible. EES proponents argue that this is what has occurred with the assumptions of gene-centrism and fractionation. Though central in standard textbook presentations of evolutionary theory (Love, 2010; Provine, 1971; Thompson, 1983), gene-centrism and fractionation are merely useful idealisations. Understood as such, the EES not only identifies gene-centrism and fractionation as contingent assumptions, but also demonstrates the value of adopting alternative ones.

4. Comparing and evaluating the EES

So far, so irenic. Yet the agenda-based strategy does not reduce all disagreement to a frictionless pursuit of different research aims. There are opportunities for genuine conflict, but the agenda-based approach suggests that these will predominantly be local in character—relativized to particular research questions. Instead of a picture where concepts are evaluable on the basis of greater or lesser empirical content, an agenda-based approach evaluates empirical aptness in the pursuit of particular research questions. This may mean that the most valuable and epistemically fruitful concepts are those with limited empirical content, yet which are appropriate for solving pressing research questions. Conflict occurs on this approach when different methods are proposed for answering the same research question—that is, when different methods are put in the service of the same aim. Here there can be disagreements as to the empirical aptness of the concepts and methods employed.

The devil, however, is always in the details—and the difficulty of the agenda-based approach comes in reconstructing both the problem agendas and means of evaluating of empirical aptness for specific research aims. When it comes to the EES, this is difficult not only because of the evolving structure of their theoretical resources and the qualitative way in which these are articulated, but also because problem agendas are themselves complex entities. Yet this is where work needs to be undertaken to evaluate the EES. In the next section, I engage in just this work by reconstructing a set of problems around the concept of niche construction. This case study illuminates the EES problem agenda, and in so doing, demonstrates some of the difficulties that the EES has had in motivating its broader reforms. As I show, in some places the EES adopts the standards, theories, models, and assumptions of standard consensus practice. In other places, they motivate new methods and concepts to pursue a research aim shared with consensus practice. The latter is where the empirical merits of the EES and consensus practice can be compared.

4.1. A case study: niche construction

Speaking generally, work on niche construction looks at the evolutionary effects of reciprocal causal relationships between organisms and their environment (Odling-Smee, Laland, & Feldman, 2003). Yet like the broader EES framework in which it features, niche construction is touted by proponents as offering a radically different vision of evolutionary change, while sceptics see it as a catch-all term for a number of already well-understood phenomena (Buskell, 2019). Debates around niche construction thus serve a useful microcosm of the larger controversy surrounding the EES.

There are islands of agreement amidst the general discord: both proponents and opponents agree organismic activity can have knock-on

consequences for evolutionary change (Laland et al., 2014; Wray et al., 2014) and recognise the growing field of research that models complex organism-environment dynamics.

Nonetheless there is broad disagreement about the theoretical implications of niche construction. Proponents argue that niche construction requires the building of models, narratives, and theories that can better accommodate the reciprocal causal relationships between organisms and their environments (Odling-Smee et al., 2003; Laland et al., 2013a, b; Laland, 2015). Such reform may also require recognising niche construction as an evolutionary process (Laland, 2015; Odling-Smee et al., 2003; Okasha, 2005), for instance, according to one recent construal, intermediate in character between natural selection and artificial selection (Laland, Odling-Smee, & Endler, 2017). Sceptics, however, deny that niche construction identifies a new kind of evolutionary process. Instead, they argue that the concept merely highlights co-variation between environmental selection pressures and trait fitnesses. More pointedly, sceptics deny that niche construction motivates the vision of evolutionary change put forward by the EES, where organismic activity significantly influences evolutionary trajectories. As numerous critics have pointed out, many niche construction models—especially those put forward by Laland and co-authors (e.g. Laland, Odling-Smee, & Feldman, 1999, 1996; Odling-Smee et al., 2003)—employ standard population genetic models.¹⁰ At least *prima facie*, this would seem to reinforce gene-centrism and standard evolutionary theory.

So if niche construction is supposed to motivate theoretical, methodological, and conceptual change to evolutionary theory, why do its models appear so rearguard? Here I turn to consider a recent paper by Uller and Helanterä (2019) which provides a sensitive reconstruction of the motivations for, and reactions against, niche construction. Uller and Helanterä argue that the conflicting interpretations of niche construction come down to whether one assumes fractionation.¹¹ While EES proponents deny fractionation, sceptics adopt it. Fractionation, recall, is the idea that evolutionary processes represent autonomous domains of activity, whose behaviour can be modelled as separate processes—often as sequential steps—in evolutionary models. Uller and Helanterä hold that the logic of fractionation entails a gene-centric interpretation of niche construction.

This gene-centric picture is one where niche construction generates salient environmental changes only by means of changing underlying gene frequencies; niche construction is akin to an ‘extended phenotype’ (Dawkins, 1982), where the phenotypic expression of genes takes place beyond the boundaries of individual organisms. Because fractionation supports a picture of evolution as the stepwise linkage of autonomous processes, the effects of niche construction must be understood in terms of previous rounds of selection or drift. Only these processes result in new variation whose expression leads to salient co-variation between traits and niche-constructing consequences on fitness.

On the alternative EES picture, the idea of causally autonomous processes is abandoned. Rather than holding that evolution involves causally distinct domains of activity, EES proponents argue that evolutionary processes are fundamentally intertwined: “individuals respond to their environment during ontogeny, and these responses shape future experiences and environments for the individuals themselves and their descendants in ways that affect their survival and reproduction.”

¹⁰ E.g. Okasha, 2005; Scott-Phillips et al., 2011; Dickins & Rahman, 2012; Dickins & Barton, 2013; Scott-Phillips et al., 2014; Gupta et al., 2017a, b. Cf. Feldman, Odling-Smee, & Laland, 2017.

¹¹ They unfortunately refer to fractionation as ‘quasi-independence’. This use is unfortunate as many researchers follow Lewontin (1978) in using ‘quasi-independence’ to describe how traits must be able to evolve (somewhat) independently from one another in to be a target for selection. Following Walsh (2015), Uller and Helanterä’s definition diverges from this common usage by taking ‘quasi-independence’ to refer to the assumption of conceptual, causal, and methodological separation between the component processes of evolution.

(Uller and Helanterä, 2019 365). By rejecting the causal autonomy of evolutionary processes, EES proponents hold that niche construction can play a vital role in shaping developmental outcomes and adaptive change; that “niche construction is both a cause and a consequence of evolution.” (Uller and Helanterä, 2019 358)

I think that Uller and Helanterä are right to diagnose assumptions around fractionation as underpinning many of the disagreements between EES proponents and sceptics. Yet however perspicacious, this diagnosis does not help us to understand the empirical issues at stake. Here I suggest that rather than there being a single issue to which niche construction is applicable, there are in fact two distinct research aims that the concept is being used to address—and that when these two aims are disentangled, we are better able to discern where the EES conflicts with standard consensus practice and where it does not.

Niche construction theorists make a number of important distinctions when introducing the concept. One is that between *inceptive* and *counteractive* niche construction. These terms refer to the positive or negative impact of niche construction on selection pressures: inceptive niche construction is where organismic activity increases the selection coefficients for a particular trait or traits, while counteractive niche construction leads to a decrease or ‘buffering’ effect on such coefficients. A second key distinction occurs between kinds of behaviours that generate niche constructing behaviour. *Perturbational* niche construction occurs when organisms change their environment, for example, by expelling waste, extracting resources, or building burrows and nests. *Relocational* niche construction, by contrast, occurs when organisms change their environment by moving to a new one. Persistent perturbational or relocational niche construction can cause organisms to experience recurrent selection pressures, insofar as organismic activity can cause populations to end up in similar ecological circumstances.

These two aspects of the niche construction concept—dynamical notions around the strength and direction of selection pressure, and evolutionary concerns about the particular traits responsible for (and perhaps selected for by) niche constructing activities—lend themselves to two distinct research aims. The first considers how traits co-vary with environments in ways that matter for evolutionary dynamics while the latter explains how organisms generate non-genetic heritable variation that influences the evolutionary trajectories of populations. While the first represents a de-idealization of common assumptions of standard population genetic models, the second points to the plasticity of development, organismic agency, and causal complexity as motivating the need for new methods, tools, and theories. Let me discuss each in turn.

As I said above, Niche construction models have typically used two-locus diallelic population genetic models where one set of alleles control environmental parameters correlated with the fitness of alleles at a second locus (Han & Hui, 2014; Hui & Yue, 2005; Laland et al., 1999, 1996; Odling-Smee et al., 2003). Even those that models that diverge from standard population genetic models retain a gene-centric framing for modelling evolutionary change (e.g. Kyllafis & Loreau, 2008). This is unsurprising: modelling traditions within evolutionary theory often partition causes of selection pressures into genetic and non-genetic causes—and on this view, niche construction represents a non-genetic selection pressure whose strength is modulated by other genetic variation. Niche construction modellers adopt this causal partitioning in part because it serves as a useful means for modelling covariation and feedback between genetic traits and environments (Odling-Smee et al., 2003).

These models and assumptions buy into a research goal and research methods shared with consensus practice. In constructing, analysing, and publishing niche construction models, EES proponents have adopted the machinery, concepts, tools, and explanatory standards of consensus practice. This is not to say that niche construction models are not novel—only that these models add causal complexity to gene-centric and fractionated models that explicitly distinguish between genetic and environmental causal effects. Here, EES researchers not only share

an aim with consensus practice, but also the latter’s evaluative standards and analytical tools.

If there is disagreement between EES proponents and sceptics here, it is that each camp holds different assumptions about the prevalence and importance of niche constructing dynamics (e.g. Wray et al., 2014). Yet as should be clear, this disagreement is made on the back of more profound agreement around concepts, methods, and means of evaluation. When it comes to exploring evolutionary dynamics, EES proponents adopt goals and standards of empirical aptness from consensus practice.

Turning to consider the role of niche construction in exploring *evolvability*, however, reveals a different situation. *Evolvability* characterises the complex dispositional property of populations to explore evolutionary possibilities (Brown, 2014; Love, 2003). Evolutionary trajectories characterise paths through these possibilities. For EES proponents, niche construction represents just one of many possible effects on evolvability, alongside other sources of non-genetic inheritance. EES sceptics, on the other hand, focus primarily on the relationship between genetic variation and changing environmental circumstances.

To illustrate this, let me adopt and analyse a central example used by Uller and Helanterä. In a compelling study, Hoekstra, Hirschmann, Bundley, Insel, and Crossland (2006) identified a single nucleotide polymorphism that changes the expression of coat colour in beach mice, causing the mice to have a lighter coat. This lighter coat allows the mice to better blend in with the sandy environment of the beach and avoid aerial predation. Inland mice who scurry on darker inland substrates lack, or have fewer copies of, these modified genes. Hoekstra and colleagues’ study thus provided compelling evidence of a single base-pair mutation that generates fitness differences, which in turn explains the representation of gene copies across geographically distinct populations.

While not denying Hoekstra and colleagues’ impressive research, Uller and Helanterä deny that the genetically driven coat colour changes are the only possible evolutionary trajectory that beach mice could have taken. Considering a range of counterfactual evolutionary trajectories, they argue that beach mice could have altered their behaviour (becoming more risk averse, altering foraging times), modified their environment (constructing burrows or safer nests), or moved to an entirely different environment. To Uller and Helanterä, these possibilities represent viable evolutionary trajectories that could have occurred through mechanisms of social learning, epigenetic modification, or niche construction—in short, from non-genetic heritable variation.

For Uller and Helanterä, the punchline is that “surviving mice are those mice for which there is a match between the context that makes a particular phenotype become expressed and the context that makes the phenotype functional.” (365) When one conceives of development as being open-ended and plastic, and where organisms can modify their environment by perturbing it or moving around within it, organisms are free to change both their phenotypes and the context in which those phenotypes are expressed. In short, by focusing on a wider range of ultimate causes arising from non-genetic inheritance, researchers may be better able to formulate salient explanatory contrasts, reconstruct past evolutionary histories, and understand the possible evolutionary trajectories that populations may traverse in the future.

Both EES proponents and sceptics agree that *evolvability* is a complex dispositional property—one that can be partitioned into different causal factors (Brown, 2014). Yet the ways in which the two camps account for these causal factors generates different conceptions and research questions concerning the nature of evolutionary trajectories. For EES sceptics, *evolvability* can be partitioned into genetic variation and environmentally induced selection pressures, with the two jointly delimiting the space of possible evolutionary outcomes. For EES proponents, the plasticity of development combined with non-genetic inheritance degrades this sharp boundary between organisms and environments. Because “the developing organism cannot be reduced to

separable components” (Laland et al., 2015, p. 6), a wider range of causal contrasts must be considered to explain the evolutionary trajectories that populations traverse. For EES proponents, while genetic variation is important in this explanatory endeavour, it is often insufficient to provide satisfactory explanations of the actual phenotypes that organisms express or could achieve (Sultan, 2015).

Issues around evolvability thus represent a genuine source of empirical friction. While both proponents and sceptics agree on the research aim being addressed—demarcating the possible space of evolutionary possibilities and explaining the actual trajectories taken—they differ in their beliefs as to the aptness of the concepts, tools, and theories needed to approach it; particularly, how these establish satisfactory explanations. For standard evolutionary theory, possible evolutionary trajectories result from the context-dependent expression of genes. Though environments shift the genetic variation of populations by changing developmental outcomes and shifting selection pressures, ultimately, it is genetic variability that explains evolutionary outcomes. Contrast this with the EES position. Here, developmental plasticity requires the consideration of multiple causes and sources of inheritance whose joint effects generate phenotypes. These causes persist for longer-or-shorter durations of time—nonetheless, this does not mean that they can be ignored. Even if the heritability of non-genetic resources only have their effects over a few generations, these can further shift downstream environmental, developmental, and genetic variation.

4.2. Niche construction, evolvability, and causal complexity

The EES approach permits a wider range of explanatory causes to serve as satisfactory explanations of evolutionary trajectories—I've here focused on niche construction, but have emphasised throughout the different kinds of causes and sources of inheritance appealed to by proponents. The experimental work by Schwab and colleagues exemplifies what such explanations might consist in: the systematic and structured cultivation of early developmental environments that play a non-trivial role in determining mature morphology and fitness. Nonetheless, standard gene-centric stories have their place as well. While EES proponents are sceptical that gene-centric explanations always give satisfactory explanations of evolutionary trajectories, they acknowledge that environmentally-driven changes in gene frequencies can be difference-making across a wide range of evolutionary scenarios.

These scenarios represent one end of a continuum where niche construction and developmental effects can be mostly ruled out. Sand hoppers like *Talitrus saltator* spend the day buried in sands above the high watermark, emerging at night to feed on decaying seaweed. The effects of the daily activities of sand hoppers on their local ecology is minimal—their burrows often collapse into the sand as they emerge, and their physiological activity makes a negligible effect on the organisms that wash on to the beach as food. It seems unlikely that niche constructing activities would explain much about the sand hoppers' evolutionary history or future potential.

But contrast sand hoppers with earthworms. The physiology of earthworms is poorly suited to deal with terrestrial concentrations of salt and water, with their kidneys being better suited to the moisture and salt content of fresh water. Yet earthworms thrive in a terrestrial environment. Why is this? The explanation for these seemingly conflicting circumstances comes down to niche construction: earthworms continually construct an environment suited to their physiology. While tunnelling through the soil, earthworms excrete mucus, pull down leaf-litter, and eliminate calcite. In so doing, they create well-aggregated soils—an environment where they are better able to take up water into their bodies (Laland and Sterelny 2006; Odling-Smee et al., 2003). For the earthworm, greater attention to organismic activity, developmental history, and niche construction seems required. Explaining their evolution seems to require appeal to past earthworm activity and how these cultivated an environment where their kidneys were buffered from selection pressures.

This is not to say that gene-centric pictures gain no purchase on stories like those of the earthworm. And were researchers to dispute the niche-constructing explanation of their aquatic-adapted kidneys, there could be genuine disagreement about the empirical aptness of concepts like niche construction for investigating and explaining the evolutionary history and evolvability of earthworms. Yet such evaluations are invariably local to specific research objectives. And while broad implications about such concepts may follow from local disagreements, they need not.

5. Conclusion

Synthesising arguments are attempts at reorganising scientific research. Here I have argued that these attempts at reorganisation motivate different problem agendas—and that when these occur within the same domain of research, these can be usefully understood as different theory presentations—that employ distinct collections of concepts, evaluative frameworks, models, and assumptions. Looking at the role of niche construction in Laland and colleagues' synthesising argument for the EES, I've shown how attending to the empirical aptness of specific concepts and methods helps to diagnose the specific research aims at stake—and thus when and where the EES conflicts with consensus practice.

The EES is an incomplete yet compelling evolutionary framework. Yet overheated rhetoric on both sides have tended to oversell the differences between the EES and consensus practice. This is not helped by the contentious historical framing put forward by proponents, which positions the EES as an alternative to the Modern Synthesis. Nor is it helped by the qualitative and pictorial form of their theoretical reflections. Taken together these features often obscure the specific research questions, empirical claims, and explanatory contrasts that differentiate the EES from consensus practice. An agenda-based approach helps to solve these problems.

Acknowledgements

Research leading to this publication was supported by a grant from the John Templeton Foundation (60501).

References

- Amundson, R. (2005). *The changing role of the embryo in evolutionary thought: Roots of evo-devo*. New York, NY: Cambridge University Press.
- Brigandt, I., & Love, A. C. (2010). Conceptualizing evolutionary novelty: Moving beyond definitional debates. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 318, 417–427.
- Brown, R. L. (2014). What evolvability really is. *The British Journal for the Philosophy of Science*, 65(3), 549–572.
- Buskell, A. (2019). Reciprocal causation and the extended evolutionary synthesis. *Biological Theory*, 14(4), 267–279.
- Cain, J. A. (1993). Common problems and cooperative solutions: Organizational activity in evolutionary studies, 1936 - 1947. *Isis*, 84(1), 1–25.
- Cain, J. A. (2009). Rethinking the synthesis period in evolutionary studies. *Journal of the History of Biology*, 42(4), 621–648.
- Carroll, R. L. (2000). Towards a new evolutionary synthesis. *TREE*, 15(1), 27–32.
- Carroll, S. B. (2005). *Endless forms most beautiful: The new science of evo devo*. New York: W. W. Norton & Co.
- Carroll, S. B. (2008). Evo-Devo and an expanding evolutionary synthesis: A genetic theory of morphological evolution. *Cell*, 134(1), 25–36.
- Charlesworth, D., Barton, N. H., & Charlesworth, B. (2017). The sources of adaptive variation. *Proceedings of the Royal Society B: Biological Sciences*, 284(1855) 20162864–12.
- Dawkins, R. (1982). *The extended phenotype: The gene as the unit of selection*. Oxford: Oxford University Press.
- Depew, D. J., & Weber, B. H. (1996). *Darwinism evolving: Systems dynamics and the genetics of natural selection*. Cambridge, MA: The MIT Press.
- Dickins, T. E., & Barton, R. A. (2013). “Reciprocal causation and the proximate–ultimate distinction. *Biology and Philosophy*, 28(5), 747–756.
- Dickins, T. E., & Rahman, Q. (2012). The extended evolutionary synthesis and the role of soft inheritance in evolution. *Proceedings of the Royal Society B: Biological Sciences*, 279(1740), 2913–2921.
- Fábregas-Tejeda, A., & Vergara-Silva, F. (2018). Hierarchy theory of evolution and the extended evolutionary synthesis: Some epistemic bridges, some conceptual rifts.

- Evolutionary Biology*, 45, 127–139.
- Feldman, M. W., Odling-Smee, J., & Laland, K. N. (2017). “Why Gupta et al.’s Critique of Niche Construction Theory Is Off Target. *Journal of Genetics*, 96(3), 505–508.
- Gardner, A. (2013). Ultimate explanations concern the adaptive rationale for organism design. *Biology and Philosophy*, 28(5), 787–791.
- Grafen, A. (1991). Modelling in behavioural ecology. In J. R. Krebs, & N. B. Davies (Eds.). *Behavioural ecology* (pp. 5–31). (3rd ed.). Oxford: Blackwell Scientific Publications.
- Griesemer, J. (1984). “Presentations and the status of theories.” *PSA. Proceedings of the Biennial Meeting of the Philosophy of Science Association*, 102–114 1984.
- Gupta, M., Prasad, N. G., Dey, S., Joshi, A., & Vidya, T. N. C. (2017a). Niche construction in evolutionary theory: The construction of an academic niche? *Journal of Genetics*, 96(3), 491–504.
- Gupta, M., Prasad, N. G., Dey, S., Joshi, A., & Vidya, T. N. C. (2017b). Feldman et Al. Do protest too much, we think. *Journal of Genetics*, 96(3), 509–511.
- Han, X., & Hui, C. (2014). Niche construction on environmental gradients: The formation of fitness valley and stratified genotypic distributions. *PLoS One*, 9(6), e99775. <https://doi.org/10.1371/journal.pone.0099775>.
- Hoekstra, H. E., Hirschmann, R. J., Bundley, R. A., Insel, P. A., & Crossland, J. P. (2006). A single amino acid mutation contributes to adaptive beach mice color pattern. *Science*, 313(5783), 101–104.
- Hui, C., & Yue, D. (2005). Niche construction and polymorphism maintenance in meta-populations. *Ecological Research*, 20, 115–119.
- Jablonka, E., & Lamb, M. (2005). *Evolution in four dimensions: Genetic, epigenetic, behavioral, and symbolic variation in the history of life*. The MIT Press.
- Kitcher, P. (1981). Explanatory unification. *Philosophy of Science*, 48(4), 507–531.
- Kitcher, P. (1989). Explanatory unification and the causal structure of the world. In P. Kitcher, & W. C. Salmon (Eds.). *In scientific explanation* (pp. 410–505). Minneapolis: University of Minnesota Press.
- Kitcher, P. (1993). *The advancement of science: Science without legend, objectivity without illusions*. Oxford: Oxford University Press.
- Kuhn, T. S. (1970). *The structure of scientific revolutions*. Chicago: University of Chicago Press.
- Kuhn, T. S. (1977). *The essential tension*. Chicago: University of Chicago Press.
- Kuratani, S., Kuraku, S., & Nagashima, H. (2011). Evolutionary developmental perspective for the origin of turtles: The folding theory for the shell based on the developmental nature of the carapacial ridge. *Evolution and Development*, 13(1), 1–14.
- Kylafis, G., & Loreau, M. (2008). Ecological and evolutionary consequences of niche construction for its agent. *Ecology Letters*, 11, 1072–1081.
- Lakatos, I. (1978). In J. Worrall, & G. Currie (Eds.). *The methodology of scientific research programmes*. Cambridge: Cambridge University Press.
- Laland, K. N. (2015). On evolutionary causes and evolutionary processes. *Behavioural Processes*, 117, 97–104.
- Laland, K. N. (2017). *Darwin’s unfinished symphony: How culture made the human mind*. Princeton: Princeton University Press.
- Laland, K. N. (2018). “Evolution unleashed” *aeon*. [online]. Available at: <https://aeon.co/essays/science-in-flux-is-a-revolution-brewing-in-evolutionary-theory>, Accessed date: 22 May 2019.
- Laland, K. N., & Kim, S. (2006). Seven reasons (not) to neglect niche construction. *Evolution*, 60(9), 1751–1762.
- Laland, K. N., Kim, S., Odling-Smee, J., Hoppitt, W., & Uller, T. (2011). “Cause and effect in biology revisited: Is mayr’s proximate-ultimate dichotomy still useful? *Science*, 334, 1512–1517.
- Laland, K., Odling-Smee, J., & Endler, J. (2017). Niche construction, sources of selection and trait coevolution. *Interface Focus*, 7(5), 20160147–20160149.
- Laland, K. N., Odling-Smee, F. J., & Feldman, M. W. (1996). The evolutionary consequences of niche construction: A theoretical investigation using two-locus theory. *Journal of Evolutionary Biology*, 9, 293–316.
- Laland, K. N., Odling-Smee, F. J., & Feldman, M. W. (1999). Evolutionary consequences of niche construction and their implications for ecology. *Proceedings of the National Academy of Sciences*, 96, 10242–10247.
- Laland, K. N., Odling-Smee, J., Hoppitt, W., & Uller, T. (2013a). More on how and why: Cause and effect in biology revisited. *Biology and Philosophy*, 28(5), 719–745.
- Laland, K. N., Odling-Smee, J., Hoppitt, W., & Uller, T. (2013b). More on how and why: A response to commentaries. *Biology and Philosophy*, 28(5), 793–810.
- Laland, K. N., Uller, T., Feldman, M. W., Kim, S., Müller, G. B., Moczek, A., et al. (2014). Does evolutionary theory need a rethink? Yes, urgently. *Nature*, 514, 161–164.
- Laland, K. N., Uller, T., Feldman, M. W., Kim, S., Müller, G. B., Moczek, A., et al. (2015). The extended evolutionary synthesis: Its structure, assumptions and predictions. *Proceedings of the Royal Society B: Biological Sciences*, 282(1813), 20151019.
- Laudan, L. (1977). *Towards a theory of scientific growth*. Berkeley: University of California Press.
- Lewens, T. (2010). Natural selection then and now. *Biological Reviews*, 85, 829–835.
- Lewens, T. (2015). *Cultural Evolution: Conceptual Challenges*. Oxford: Oxford University Press.
- Lewontin, R. C. (1978). Adaptation. *Scientific American*, 212–231.
- Lively, C. M. (1986c). Canalization versus developmental conversion in a spatially variable environment. *The American Naturalist*, 128(4), 561–572.
- Lively, & Curtis, M. (1986a). Competition, comparative life histories, and maintenance of shell dimorphism in a barnacle. *Ecological Economics*, 67(4), 858–864.
- Lively, & Curtis, M. (1986b). Predator-induced shell dimorphism in the acorn barnacle *Chthamalus anisopoma*. *Evolution*, 40(2), 232–242.
- Love, A. C. (2003). Evolvability, dispositions, and intrinsicity. *Philosophy of Science*, 70(5), 1015–1027.
- Love, A. C. (2010). Rethinking the structure of evolutionary theory for an extended synthesis. In M. Pigliucci, & G. B. Müller (Eds.). *Evolution: The extended synthesis* (pp. 403–442). Cambridge, MA: The MIT Press.
- Love, A. C. (2013). Theory is as theory does: Scientific practice and theory structure in biology. *Biological Theory*, 7(4), 325–337.
- Love, A. C. (2017). Evo-devo and the structure(s) of evolutionary theory: A different kind of challenge. In P. Huneman, & D. M. Walsh (Eds.). *Challenging the modern synthesis: Adaptation, development, and inheritance* (pp. 159–187). Oxford: Oxford University Press.
- Lynch, M. (2007). *The origins of genome architecture*. New York: Sinauer Associates.
- Milam, E. L. (2010). The equally wonderful field: Ernst mayr and organismic biology. *Historical Studies in the Natural Sciences*, 40(3), 279–317.
- Mokady, O., Mizrahi, L., Perl-Treves, R., & Achituv, Y. (2000). The different morphs of *Chthamalus anisopoma*: A phenotypic response? Direct molecular evidence. *Journal of Experimental Marine Biology and Ecology*, 243, 295–304.
- Müller, G. B. (2007). Evo-Devo: Extending the evolutionary synthesis. *Nature Reviews Genetics*, 8, 943–949.
- Müller, G. B., & Pigliucci, M. (2010). Elements of an extended evolutionary synthesis. In M. Pigliucci, & G. B. Müller (Eds.). *Evolution: The extended synthesis* (pp. 3–17). Cambridge, MA: The MIT Press.
- Nagashima, H., Sugahara, F., Takechi, M., Ericsson, R., Kawashima-Ohya, Y., Narita, Y., et al. (2009). Evolution of the turtle body plan by the folding and creation of new muscle connections. *Science*, 325(5937), 193–196.
- Odling-Smee, J., Laland, K. N., & Feldman, M. W. (2003). *Niche construction: The neglected process in evolution*. Princeton: Princeton University Press.
- Okasha, S. (2005). On niche construction and extended evolutionary theory. *Biology and Philosophy*, 20(1), 1–10.
- Okasha, S. (2011). Theory choice and social choice: Kuhn versus Arrow. *Mind*, 120(477), 83–115.
- Oyama, S. (2000). *The ontogeny of information*. Durham, NC: Duke University Press.
- Parker, E. S., Dury, G. J., & Moczek, A. P. (2019). Transgenerational developmental effects of species-specific, maternally transmitted microbiota in *Onthophagus* dung beetles. *Ecological Entomology*, 44(2), 274–282.
- Pievani, T. (2012). An evolving research programme: The structure of evolutionary theory from a lakatosian perspective. In A. Fasolo (Ed.). *The theory of evolution and its impact* (pp. 211–228). Dordrecht: Springer.
- Pigliucci, M. (2007). Do we need an extended evolutionary synthesis? *Evolution*, 61(12), 2743–2749.
- Pigliucci, M. (2008). Is evolvability evolvable? *Nature Reviews Genetics*, 9, 75–82.
- Pigliucci, M. (2009). An extended synthesis for evolutionary biology. *Annals of the New York Academy of Sciences*, 1168, 218–228.
- Provine, W. B. (1971). *The origins of theoretical population genetics*. Chicago: University of Chicago Press.
- Raff, R. (1996). *The shape of life: Genes, development, and the evolution of animal form*. Chicago: University of Chicago Press.
- Rieppel, O. (2001). Turtles as hopeful monsters. *BioEssays*, 23, 987–991.
- Robert, J. S. (2004). *Embryology, epigenesis, and evolution: Taking development seriously*. Cambridge: Cambridge University Press.
- Rosenberg, A., & Bouchard, F. (2015). Fitness. In E. N. Zalta (Ed.). *Stanford encyclopedia of philosophy* <https://plato.stanford.edu/entries/fitness/>.
- Schöll, R., & Pigliucci, M. (2015). “The proximate–ultimate distinction and evolutionary developmental biology: Causal irrelevance versus explanatory abstraction. *Biology and Philosophy*, 1–18.
- Schwab, D. B., Casasa, S., & Moczek, A. P. (2017). Evidence of developmental niche construction in dung beetles: Effects on growth, scalin and reproductive success. *Ecology Letters*, 20, 1353–1363.
- Schwab, D. B., Riggs, H. E., Newton, I. L. G., & Moczek, A. P. (2016). Developmental and ecological benefits of the maternally transmitted microbiota in a dung beetle. *The American Naturalist*, 188(6), 679–692.
- Scott-Phillips Thomas, C., E Dickins, T., & West, S. A. (2011). Evolutionary theory and the ultimate-proximate distinction in the human behavioral sciences. *Perspectives on Psychological Science*, 6(1), 38–47.
- Scott-Phillips, Thomas, C., Laland, K. N., Shuker, D. M., E Dickins, T., & West, S. A. (2014). The niche construction perspective: A critical appraisal. *Evolution*, 68(5), 1231–1243.
- Smocovitis, V. B. (1996). *Unifying biology: The evolutionary synthesis and evolutionary biology*. Princeton: Princeton University Press.
- Sober, E. (1975). *Simplicity*. Oxford: Clarendon Press.
- Sultan, S. (2015). *Organism and environment: Ecological development, niche construction, and adaptation*. Oxford: Oxford University Press.
- Tanghe, K. B., De Tiège, A., Pauwels, L., Blancke, S., & Braeckman, J. (2018). “What’s wrong with the modern evolutionary synthesis? A critical reply to Welch. *Biology and Philosophy*. <https://doi.org/10.1007/s10539-018-9633-3> 2017.
- Thompson, P. (1983). The structure of evolutionary theory: A semantic approach. *Studies in History and Philosophy of Science*, 14(3), 215–229.
- Uller, T., and Helanterä. 2019. *Forthcoming*. “Niche construction and conceptual change in evolutionary biology.” *The British Journal for the Philosophy of Science*, 70: 351–375.
- Walsh, D. (2015). *Organisms, agency, and evolution*. Cambridge: Cambridge University Press.
- Welch, J. J. (2017). “What’s wrong with evolutionary biology? *Biology and Philosophy*, 32(2), 263–279.
- Wray, G. A., Hoekstra, H. E., Futuyma, D. J., Lenski, R. E., Mackay, T. F. C., Schluter, D., et al. (2014). Does evolutionary theory need a rethink? No, all is well. *Nature*, 514, 161–164.