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REVIEW

The Extended Evolutionary Synthesis: what is the debate about, and what might success for the extenders look like?

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Debate over the Extended Evolutionary Synthesis (EES) ranges over three quite different domains of enquiry. Protagonists are committed to substantive positions regarding (1) empirical questions concerning (for example) the properties and prevalence of systems of epigenetic inheritance; (2) historical characterizations of the modern synthesis; and (3) conceptual/philosophical matters concerning (among other things) the nature of evolutionary processes, and the relationship between selection and adaptation. With these different aspects of the debate in view, it is possible to demonstrate the range of cross-cutting positions on offer when well-informed evolutionists consider their stance on the EES. This overview of the multiple dimensions of debate also enables clarification of two philosophical elements of the EES debate, regarding the status of niche-construction and the role of selection in explaining adaptation. Finally, it points the way to a possible resolution of the EES debate, via a pragmatic approach to evolutionary enquiry.

ADDITIONAL KEYWORDS: Darwin – evolution – modern synthesis – neoDarwinism.

LEVELS OF EXTENSION

This review attempts to clarify what is at stake in the debate over the Extended Evolutionary Synthesis (EES) and extends the early exploration of the debate by Pigliucci & Müller (2010). Laland *et al*. (2014: 161–162) are convinced that, 'the EES will shed new light on how evolution works'. In response, Wray *et al*. (2014: 164) insist that, 'We, too, want an extended evolutionary synthesis, but for us, these words are lowercase because this is how the field has always advanced.' Everyone agrees that extensions – of some kind, at least – to current evolutionary understanding will be illuminating. Everyone agrees on the value of the approaches to evolutionary study that have gone before. Each side nonetheless regards the other as deeply mistaken. Some exchanges have been full of suspicion regarding the motives of those holding opposing views (Gupta *et al*., 2017; Feldman *et al*., 2017). A newcomer to this mêlée – even if well versed in the facts of evolution – may wonder what the fuss is about. It had better concern more than a preference for capital letters.

EES enthusiasts tend to recommend revised approaches to such diverse biological phenomena as inheritance, adaptation and development. I argue that the debate goes much further. The main protagonists are committed to substantive historical views regarding the nature of evolutionary theory from the late 1910s onwards, the flexibility of the investigative and explanatory tools that have been developed by evolutionary biologists, and the openness of research communities to novel approaches. They take stands on conceptual and philosophical questions concerning (among other things) what an evolutionary process is, the nature of biological causation and how adaptation should be explained. Finally, the groups discussing the EES differ on straightforward empirical questions relating to such things as the properties of epigenetic

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inheritance systems. In other words, we can discern disputes over three analytical domains: the historical, the conceptual/philosophical and the empirical.

The factional nature of this debate invites evolutionists either to support the EES or to oppose it. The diversity of broad themes and sub-topics under discussion suggests, however, that thoughtful researchers are unlikely to fall into two neat camps. We should expect cross-cutting verdicts regarding (for example) the significance of epigenetic inheritance, the constraining nature of the Modern Synthesis (MS), the proper characterization of evolutionary processes, and the role of selection in explaining adaptation.

The primary goal of this paper, then, is to demonstrate how many distinct disputes are being conducted under the umbrella of the EES debate. It is not possible in a single article to come to detailed verdicts regarding them all. This taxonomy of disputes is useful all the same, because the first step to resolving argument over the EES is to understand what the debate is about. The article moves on to focus on conceptual aspects of the disputes over niche-construction and adaptation, understood as exemplars for the wider debate. In particular, it offers a deflationary resolution of the dispute over whether niche-construction is an evolutionary 'process'. Finally, it uses the question of what success for the extenders would look like to sketch a potential resolution of the EES debate that should be acceptable to all camps.

RADICALS VERSUS ACCRETIONISTS

EES advocates call for change. What sort of changes are these, how radical are they intended to be and what are they changes to?

The phrase 'Extended Evolutionary Synthesis' might seem to imply that the changes are envisaged as simple extensions of, or supplements to, an evolutionary synthesis whose core can remain intact. In fact, proponents of the EES usually aim for profound revisions that cannot be understood as simple progress by accretion. For this reason I refer to EES enthusiasts as 'radicals'. They have repeatedly resisted being labelled as 'revolutionaries', and in using the term 'radicals' I mean to imply neither that they believe change should be very rapid, nor that they all advocate reform of the entire evolutionary community, only that the changes they would like to see run deep.

EES defenders maintain that enormous achievements have been made via evolutionary approaches formulated in the broad style of Fisher, Wright, Dobzhansky, Maynard Smith, Hamilton and many others from the 1920s onwards. Even so, they believe that an evidential and conceptual case has been accumulating for significant revisions to the orienting framework inherited from such theorists. The EES, 'is not just an extension of the MS but a distinctively different framework for understanding evolution …' (Laland *et al*., 2015: 3).

Different EES advocates give different emphases regarding how disruptive the proposed changes will be. Laland (2018) explains that he knows, 'of no biologist who wants to rip up the textbooks, or throw out natural selection.' The EES is meant to consist in continuous, not revolutionary, change with respect to the modern synthesis: 'what is going on is "normal science".' Moreover, Laland stresses the insights that will emerge if some biologists work under the guidance of an extended synthesis. He does not argue that all others should cease to work within a more traditional perspective. Thus, he advocates a form of parallel-track pluralism, which gives explicit credit to the philosopher of science Imre Lakatos, in preference to the picture of revolutionary paradigm shifts advocated by Thomas Kuhn (Fábregas-Tejeda & Vergara-Silva, 2018). There are radical elements to his proposals all the same, because in seeking a broader understanding of 'the causes of evolution', he believes this 'changes how we think about the process as a whole' (Laland, 2018).

Müller places less stress on pluralism. He argues that the accumulation of new evidence and theory about a range of sub-topics such as epigenetic inheritance, developmental plasticity and the origins of adaptive novelties brings with it a basic conceptual re-orientation of evolutionary theory's core. As he explains, 'The term "EES" used here and elsewhere … is not meant as a simple extension of the MS, as is sometimes wrongly implied, but to indicate a comprehensive new synthesis' (Müller, 2017: 8). Müller is not calling for well-known textbooks to be ripped up, but it does seem that he would like to see those textbooks subject to significant restructuring.

The EES's opponents have objected to these calls for basic change in underlying theoretical orientation. I refer to them as 'accretionists'. The likes of Wray *et al*. (2014) and Futuyma (2017) do not believe that evolutionary theory should remain static in all respects. However, they anticipate that evolutionary biology will progress via elaborations of underlying theoretical and explanatory structures that have long been entrenched in evolutionary theory. They see no need at present for what we might think of as fundamental reforms to these basic structures [see Love (2017) for different understandings of what the 'structure' of our biological knowledge might amount to].

FROM EMPIRICAL TO HISTORICAL QUESTIONS

Empirical controversies in the EES

It hardly needs stating that some disputes between radicals and accretionists concern empirical matters. To pick just one example, Charlesworth *et al.* (2017) have countered the radicals regarding the evolutionary significance of non-genetic forms of inheritance. Part of their case rests on their view that there is little evidence of the relevant forms of non-genetic transmission being widespread in nature. They acknowledge that small-interfering RNAs may constitute a non-nuclear means whereby adaptive traits acquired in response to an environmental challenge can be passed to subsequent generations. Moreover, they cite cytoplasmic inheritance of infection resistance in *Caenorhabditis elegans*, mediated via such small-interfering RNAs, as an empirically plausible example of such inheritance. Yet they caution that, 'it remains to be determined how frequently such processes occur in nature' (Charlesworth *et al.*, 2017: 4). Their general contention, then, is that a good empirical case for the widespread operation of non-genetic forms of inheritance is still lacking. Meanwhile, the radicals come to a quite different assessment of the evidence (Laland *et al.*, 2015; see also Jablonka & Lamb, 2014 for a thorough survey of forms of non-genetic inheritance from the perspective of researchers highly sympathetic to the EES). An early example of experimental work on non-genetic inheritance comes from Beisson & Sonneborn (1965). Their work is reviewed under the category of 'structural inheritance' by Jablonka & Lamb (2014).

This debate remains open: recent reviews on the significance of non-genetic inheritance have come to a range of conclusions from scepticism (Otterdijk & Michels, 2016) to optimism (Bohacek & Mansuy, 2015) via various more guarded approaches. Miska & Ferguson-Smith (2016: 59), for example, note that while there is a clear case for non-genetic inheritance in many plant and animal organisms, 'In mammals, the molecular mechanisms have been challenging to elucidate'. Gapp & Bohacek (2018: 1) remark that even for mammals, 'While [the] concept of epigenetic germline inheritance has long been met with skepticism, evidence in support of this route of information transfer is now overwhelming, and some key mechanisms underlying germline transmission of acquired information are emerging.' Sometimes, then, disputes between radicals and accretionists look to first-order empirical questions, and the debate is likely to be clarified as further evidence accumulates. However, EES debates do not stop with such empirical questions, as we will now see.

The historical legacy of the Modern Synthesis

The conceptual topics discussed by EES protagonists are comparatively well known, and some of their major themes will be explored later in this review. It is perhaps less obvious that EES debates also concern historical questions, as this section establishes. Explicit recognition of the historical controversies that are implicated in the EES comes from Minelli (2010), Love (2017), Fábregas-Tejeda & Vergara-Silva (2018), Baedke (2018) and Griesemer (2019).

To show the need for revisions to the evolutionary mainstream, EES advocates must achieve two distinct tasks. A conceptual and empirical case has to be made for the nature of the evolutionary processes that require a new synthesis. A historical case also needs to be made for the character of the discipline in need of revision. For example, suppose that the discipline of evolutionary biology as a whole is already poised to accept the full significance of phenomena such as epigenetic inheritance or niche-construction. Suppose, further, that it already possesses many of the tools required to understand these processes, and that any new tools it may need can be fashioned via slight modifications to mainstream techniques for modelling, empirical investigation and so forth. While emergent empirical evidence might provoke increasing recognition of how widespread such phenomena are, no reworking of basic frameworks will be required.

This is why major statements of the EES – and major efforts to rebut them – begin with lengthy historical characterizations of evolutionary biology. Laland *et al.* (2014: 164), for example, claim that, 'The core of the current evolutionary theory was forged in the 1930s and 1940s.' They describe this core in terms of 'tenets', 'assumptions' or the 'story that [standard evolutionary theory] tells': new variation is a consequence of random genetic mutation, inheritance is a matter of the passing on of DNA and natural selection is the sole cause of adaptation. There is a similar characterization in Laland *et al.*'s (2015: 1–2) more detailed presentation: the Modern Synthesis 'has provided the dominant conceptual framework for evolutionary biology', and this framework consists, again, in a series of 'assumptions'. In other words, the framework should be understood in terms of a series of general assertions or hypotheses about evolutionary processes.

There are three important elements to this broad historical characterization: first, it is possible to pin down a fairly well-characterized episode in the 1930s and 1940s in which a synthetic approach to evolution was forged; second, this 'Modern Synthesis' is best understood as a series of assumptions about the general nature of evolutionary processes; third, these same assumptions have continued to provide the core of evolutionary biology up to the present day.

Accretionists sometimes agree with all three aspects of the radicals' historical picture. Charlesworth *et al*. (2017: 1) claim that the 'basic ideas' of the MS 'remain central to contemporary biology, despite enormous advances over the past 80 years …'. They, too, think that the MS should be characterized in terms of tenets elaborated in the 1930s and 1940s and maintained ever since. Their particular concern is to show that all is well with the claim that, 'adaptive evolution is due to natural selection acting on heritable variability that originates through accidental changes in the genetic material' (Charlesworth *et al*., 2017: 1). Here the accretionists endorse the radicals' historical claim that modern evolutionary theory has inherited, more or less intact, a group of general organizing claims about nature that were first formed 80 years ago. Disagreement instead concerns whether these claims are accurate.

It is possible, however, to detect an additional line of debate that concerns the radicals' characterization of history. Wray *et al*. (2014: 163) assert that since the 1930s and 1940s, 'generations of evolutionary biologists have modified, corrected and extended the framework of the modern synthesis in countless ways'. Their view is that, 'What Laland and colleagues term the standard evolutionary theory is a caricature that views the field as static and monolithic …' (see also Futuyma, 2017: 1). In assessing this historical aspect of debate it is important to keep in mind an important distinction between the general claims we make about evolutionary processes – the assumptions, tenets or hypotheses enumerated by radicals and accretionists alike – and the tools we use to investigate nature.

EVOLUTIONARY ASSUMPTIONS AND EVOLUTIONARY TOOLS

One of the radicals' most often-repeated claims concerns the need to integrate various forms of non-genetic inheritance into the study of evolution. Helanterä & Uller (2010), for example, adopt an expanded version of the Price equation to explore the evolutionary significance of a variety of forms of inheritance – including horizontal gene transfer and various forms of epigenetic inheritance – that clearly were not envisaged by the architects of the MS. Suppose, then, that we understand the MS as a set of general assumptions or hypotheses about evolutionary processes. To the extent that Helanterä and Uller succeed in demonstrating the evolutionary importance of forms of inheritance that are at odds with the gene-focused claims of MS, then they also succeed in justifying their call for 'extending the Modern Synthesis view of genetic inheritance' (Helanterä & Uller, 2010: 2).

Remember, though, that they use an adapted version of the Price equation (owing to Frank, 1997) to ground their claims. This underlines the fact that evolutionary thinkers have already developed – since the 1970s in the case of the Price equation and its later modifications – well-established tools to explore phenomena that were not anticipated in the 1930s and 1940s. Helanterä & Uller (2010: 12) duly acknowledge that the phenomena they are interested in, 'can be incorporated in the quantitative genetics framework'.

An ambiguity in Charlesworth *et al*.'s (2017) attack on the radicals exemplifies this deeper division regarding how the evolutionary 'mainstream' is interpreted. For the most part they are concerned to deny that epigenetic inheritance systems can sustain processes of adaptation by natural selection. However, occasionally their focus seems to be different:

> Combining modes of inheritance that differ in their mutation rates and transmission patterns can alter the outcome of selection in complex ways … However, this is not of fundamental significance as far as the general properties of evolutionary dynamics are concerned. (Charlesworth *et al*., 2017: 7)

They seem to agree with radicals like Uller and Helanterä that interactions between systems of inheritance can alter outcomes of selection in ways that merit detailed investigation. What, then, do they mean by simultaneously conceding the proposal that these influences might be 'complex', while also insisting that they are not of 'fundamental significance'? They suggest that we should not lose sight of very general constraints on how natural selection explains the appearance of adaptation: however variation is inherited, the process of inheritance must be reasonably faithful and environments must be reasonably stable. The result, they say, is that the tools used for understanding evolution as it acts on genetic variation can also be used to understand evolution when it acts on other forms of inherited variation [see Lu & Bourrat (2018) for a similar defence of the traditional approach].

This underscores the difficulties in coming to any straightforward assessment of the EES debate. Someone who is convinced of the widespread action of non-genetic inheritance across numerous taxa may align themselves with the radicals when considering what difference these processes make to evolutionary outcomes. Alternatively, they may find themselves in alignment with the accretionists if they instead focus on the issue of whether mainstream evolutionary theory possesses the sorts of tools needed to explore these phenomena (Minelli, 2010). Griesemer (2019) doubts whether there could ever be the sort of uncontested account of the MS itself that would enable us to decisively assess calls for 'extensions' to it. He cites Callebaut's remark that 'such debates can go on forever. If … the Synthesis has no essence, its extensions are negotiable' (Callebaut, 2010: 458).

This possibility is demonstrated by Bonduriansky & Day (2018), whose *Extended Heredity: A New Understanding of Inheritance and Evolution* makes a detailed theoretical and empirical case for the evolutionary importance of various forms of non-genetic inheritance. They make use of the Price equation to frame these questions. They are, however, sceptics regarding the EES (Bonduriansky *et al*., 2018). In spite of championing an extended approach to inheritance – one of the themes stressed repeatedly by the radicals – Bonduriansky and Day have distanced themselves from the radicals' cause.

This phenomenon – whereby the very people whose research is, on the face of things, the most congenial to the radicals' claims, nonetheless express neutrality or scepticism towards the EES – is not especially unusual. Brakefield and collaborators have done widely admired research on developmental bias, as explored through detailed empirical investigations of butterfly eyespots (e.g. Beldade *et al*., 2002; see also Brakefield, 2006). Developmental bias is another phenomenon repeatedly stressed by the EES radicals. They use it to undermine two assumptions that they link to the MS: first, that the variation presented to selection is 'random', and second, that developmental processes cannot exert important influence on evolutionary trajectories. It is noteworthy that while Brakefield has very explicitly joined with some EES radicals in stressing the manner in which the study of bias can help to inform a variety of important evolutionary questions regarding (for example) evolvability, macroevolutionary patterns and so forth (Uller *et al*., 2018), he has not yet gone so far as to endorse any more radical claims regarding the need for a fundamental reconfiguration of dominant approaches to the study of evolution.

INTERIM SUMMARY

It is time to take stock of the argument so far. The debate over the EES is in part a historical one. It turns on whether we should construe the history of evolutionary theory in terms of a series of debates over hypotheses or assumptions regarding the nature of evolutionary processes; whether we should construe it in terms of the development and modification of various explanatory and experimental tools and techniques; or whether we should instead construe it in terms of the acceptance of scientists into growing communities of research. The EES debate is illuminated by sociological work that compares the strategic role of christening the 'Modern Synthesis' movement with current efforts to form an EES community. The paper by Fábregas-Tejeda & Vergara-Silva (2018) is recommended for further analysis. Understanding this debate helps to explain why the EES debate has been hard to resolve: the question of how one assesses the radicals' cause for reform depends on how one assesses the current and past status of the evolutionary 'mainstream' (Callebaut, 2010).

To the extent that one thinks of the mainstream as dominated by a set of assumptions that are now 80 years old, one is likely to join the radicals' cause. The work of Bonduriansky and Day gives us good reason to challenge the notion that the genetic inheritance system is the only one that matters in the study of evolution. Brakefield's work gives us good reason to think that evolutionary trajectories can be affected by the biases introduced by developmental processes into the range of available phenotypic variation.

To the extent that one instead thinks of the mainstream as dominated by a malleable and growing set of tools for modelling and understanding various evolutionary problems, one is more likely to be a sceptic. The fact that Brakefield's work is widely respected indicates that mainstream evolutionary biology has already found some ways to pursue research on developmental bias, and gives us reason to anticipate it might be able to accommodate newer techniques that simulate the action of developmental mechanisms *in silico* (e.g. Salazar-Ciudad & Jernvall, 2010). The work of Bonduriansky & Day (2018) gives us reason to think the Price equation will help us to understand non-genetic inheritance in ways that involve comparatively modest modifications to the frameworks already used for understanding genetic inheritance. This tool was not available to the early synthesis architects, but it has been in wide use for over 30 years, and it has been subject to modifications and refinements over this period.

In response to both the examples treated in this section – extended inheritance and developmental bias – EES advocates will argue that we should not lose sight of their primary contention. Their view is not that these phenomena cannot be approached from the traditional perspective of the MS. Instead, their claim is that the MS imposes restrictive constraints on how we understand them (Laland *et al*., 2015). Radicals argue that the MS encourages a conception of developmental bias as a negative constraint on selection: it can only explain the non-appearance of adaptive phenotypes we might otherwise anticipate. Instead, we should also ask how developmental biases facilitate the pursuit of adaptive pathways that would otherwise be closed off or harder to access (Uller *et al*., 2018). Similarly, they argue that the MS encourages us to ask whether extended systems of inheritance might underpin the generation of adaptation in the same manner as genetic systems of inheritance. Yet advocates of the EES point to ways in which non-genetic inheritance can act to facilitate or constrain which evolutionary pathways are followed, even when selection continues to act on iterated cycles of genetic variation. These issues reappear in the final sections of this paper, which deal in more detail with the relationship between selection and adaptation.

NICHE CONSTRUCTION AND EVOLUTIONARY PROCESSES

The causal direction of selection

The philosophical and conceptual strands of the EES debate are nicely illustrated by EES radicals' claims for niche-construction. Müller, for example, recommends the inclusion of niche-construction alongside natural selection as a basic revision to the MS (Müller, 2017). He represents the theoretical structure of the MS using a diagram that features (among many other things) an arrow labelled 'natural selection' that moves from environment to organism. His depiction of the EES features an additional arrow, labelled 'niche-construction', that moves from organism to environment.

This way of representing one of the recommended transformations to the dominant framework has intuitive appeal. It is tempting to think of natural selection as a force exerted by the environment on organisms, as when avian predators are credited with causal responsibility for reshaping a population of peppered moths. Some may be equally tempted to think that fully understanding the causal fit between moths and their environment requires that we take into account a further process, whereby moths choose where to reside. Thorpe made this argument in the 1960s, in ways that anticipate many of the EES advocates' concerns (e.g. Uller & Helanterä, 2018):

> … before an organism's environment can exert natural selection on it, the organism must select the environment to live in. That is, there is a feedback or cybernetic system in which there is nothing that is simply cause and simply effect. It is useless for melanistic moths in industrial areas to become darker unless they choose the dark patches to sit on, which in fact they do. (Thorpe, 1965: 15–16)

Radick (2017) analyses Thorpe's work in detail.

This way of presenting things encourages the proposal that selection needs to be supplemented by an additional causal process that also explains adaptation, yet which runs in the opposite direction. This way of thinking about selection – and, correlatively, about how an appeal to niche-construction augments the modern synthesis – may be intuitive, but it faces significant conceptual objections. Selection is not best understood as a directional force exerted by environments on organisms.

Exactly how natural selection should be understood is contentious (Sober, 1984; Walsh *et al.*, 2002; Reisman & Forber, 2005; inter alia). It is comparatively uncontroversial to identify selection with the existence of fitness differences in a population (Sober, 1984). That is to say, selection is present whenever there are differences in the expected reproductive outputs of the variants present in the population. The strength of selection can then be quantified according to the degree of variance in fitness (Fisher, 1930).

The differences in expected reproductive outputs that constitute selection are always the result of mutual causal interactions between organisms and their environments. Consider a mutation that causes a metabolic change, which in turn means that an organism reaches reproductive age more quickly than others in the population. This may confer a fitness advantage. Selection arises here from interactions between developmental processes and the social environment: there is no need for us to find an environmental force to identify with selection, and it would be difficult to know which environmental force we should pick. Even so, we are dealing here with an instance of 'selection' in an entirely mainstream sense of the term.

For another example, suppose that males with longer tails are more attractive to females than males with shorter tails. The result is that females are more likely to allow mating opportunities to these longer-tailed males. Selection for tail length is at work here in a manner that can be represented in mainstream evolutionary frameworks. It would be a mistake, however, to claim that selection consists in a directional causal force that runs from environment to organism, rather than a force running from organism to environment. The greater fitness of the longer-tailed variant is the result of causal interactions between male anatomy, female perceptual systems and mating behaviours. Formal approaches to selection are neutral concerning whether fitness differences arise from effects of environments on organisms, organisms on environments, or reciprocal interactions between the two.

The productivity of niche-construction

Accretionists do not usually criticise radicals by highlighting problems inherent in the directional causal conception of selection. Instead they point out that a recognition of how organisms alter their environments, and the development of tools to help understand such phenomena, are about as old as the MS itself. Odling-Smee *et al*. (2003) define niche-construction as 'the process whereby organisms … modify their own and/or each other's niches'. A niche, in turn, is the 'sum of all the natural selection pressures to which the population is exposed' (Odling-Smee *et al*., 2003: 419). Frequency-dependent selection and sexual selection are consequently instances of niche-construction. They are phenomena widely acknowledged to result in characteristic evolutionary dynamics. For example, sexual selection can explain 'runaway' phenomena, and phenomena that would otherwise appear plainly maladaptive. They are also phenomena for which explanatory mathematical machinery has long been available. The upshot, claim accretionists, is that while niche-construction is undeniably important, no revision is needed if we are to take it into account (Scott-Philipps *et al*., 2014; Wray *et al*., 2014).

Niche-construction enthusiasts give two complementary responses to accretionists' scepticism. One draws on the heuristic value of the niche-construction perspective, while the other advocates a deeper reconfiguration of how evolutionary processes should be understood.

THE HEURISTIC DEFENCE OF NICHE-CONSTRUCTION

The heuristic defence is effective against sceptics who would rather eliminate the language of niche-construction from the evolutionary lexicon. Radicals simply highlight the volume of insightful empirical research that has been inspired by the niche-construction perspective (see Feldman *et al*., 2017). It does not matter if similar insights might have been reached via approaches that eschew the term 'niche-construction', and which are not so closely aligned with the EES. These include approaches based on indirect genetic effects (e.g. Wolf *et al*., 1998), and 'eco-evolutionary dynamics' (e.g. Pelletier *et al*., 2009). The fruitfulness of the niche-construction perspective requires only that the insights it has provoked were not produced in a different way.

This defence is genuine, but modest. It does not show that the niche-construction approach is more productive overall than alternative approaches to understanding organism–environment interactions. Hence it does not give strong reasons for mainstream evolutionists to switch towards niche-construction. Recall, though, that this may not be among the radicals' goals. Laland's (2018) priority, for example, is to make a case for the ongoing productivity of the EES framework, but not in a manner that advocates closing down approaches that are more closely aligned with the MS.

There is a further limitation. We do not show that evolutionary theory's basic explanatory structures need to be revised simply by showing that several researchers have found that the niche-construction perspective offers fruitful insights. To achieve the more radical revisionary task it is necessary to show not merely that the notion of niche-construction has been inspiring for some researchers, but that it brings with it deep changes to the structure of the more dominant approach. One might argue, for example, that the heuristic value of the niche-construction perspective is explained by the more perspicacious manner in which those who use it represent underlying evolutionary processes. This is why the radicals tend to move beyond the simple heuristic defence, to focus on how niche-construction is conceptualized.

NICHE-CONSTRUCTION AS PHENOMENON AND PROCESS

In response to Gupta *et al*.'s (2017) polemic against niche-construction, the champions of niche-construction have re-asserted that it was never their intention to suggest that past evolutionists had neglected organismic influences on environments (Feldman *et al*., 2017). Instead, they argue that in addition to recognizing the *phenomena* of niche-construction – which they acknowledge have been a staple of evolutionary study ever since Darwin's work on earthworms – an extended synthesis must include niche-construction as an evolutionary *process*.

This aspect of the debate may seem puzzling. Niche-construction is obviously a process, in the banal sense that specific instances of it – the creation of dams by beavers, the building of bowers by bowerbirds – consist in events sequenced over time. These events are also of uncontroversial evolutionary importance, in the equally banal sense that they have impacts on the compositions of populations over several generations (Okasha 2005). Why, then, would anyone deny that niche-construction is an evolutionary process?

The answer (in some cases, at least) is that accretionists have a particular, and demanding, criterion in mind for what is to count as an evolutionary process. They do not deny that organisms' modifications of their environments cause changes in the composition of populations over time. Predation, parasitism and exogenous changes to physical features of environments cause evolution in the same sense. And yet, these latter series of events do not feature in the most basic textbook lists of evolutionary processes alongside selection, drift, mutation and migration. Rather, they are ways in which selection (and other genuine processes) may come about. Hence Scott-Phillips *et al*. (2014: 1233) argue that the radicals are wrong to consider niche-construction as an evolutionary process: 'Environmental change is not a "process" of evolution, and, by the same logic, neither is organismic activity … Both are instead potential sources of the genetic covariance on which natural selection acts.'

'Direct' causes of evolution

In response to such sceptical arguments, Laland *et al*. (2017: 2) have claimed that, 'Traditionally in population and quantitative genetics, we tend to restrict evolutionary processes to those processes that directly change gene frequencies.' This, they suggest, is why accretionists think of selection, but not niche-construction, as an evolutionary process. They argue that this traditional conception of an evolutionary process should be rejected, thus opening the way to a recognition of niche-construction as an evolutionary process in its own right.

I doubt that the traditional approach of population genetics truly equates evolutionary processes with 'direct' causes of gene-frequency change, even though both accretionists and radicals have suggested it does. More generally, I argue in this section that it is a mistake to use the distinction between 'direct' and 'indirect' causes as a criterion to demarcate genuine from spurious evolutionary processes. It is unclear, for example, whether drift is a 'direct' cause of trait frequency change. Even so, drift more or less always features on basic textbook lists of evolutionary factors, forces or processes. Some have argued that drift is not properly understood as a cause at all (e.g. Walsh *et al*., 2002). Instead, they say, it is deviation from expected outcome, as predicted by fitness values. Those who do consider drift to be a cause tend to do so on the basis that the intensity of drift is inversely proportional to the size – strictly speaking the effective size – of a population. Hence we can intervene on the strength of drift, in a way that makes predictable differences to a population's later composition (Reisman & Forber, 2005). This population-level conception hardly credits drift with the most 'direct' causal role in changing populations, even if it may give drift a causal role of some kind. The token organism–environment interactions that result in some kinds of individuals having lesser reproductive success than fitness values would lead us to expect – such as those lightning strikes that happen to decimate the healthiest in a population – are more 'direct' causes of the evolutionary changes attributed to drift.

Turning to the supposedly 'direct' causal role of selection, consider again a genetic mutation that increases the speed with which an organism arrives at reproductive maturity. Such a mutation could be favoured by selection. In this kind of scenario, the 'direct' causes of the mutation's spread through the population presumably include the developmental changes that increase speed of maturation. They may also include the increased number of mating events that the organism undergoes, and the increased number of births that occur over the life of the organism. Walsh (2015) draws the conclusion that far from being a direct *cause* of population change, selection is instead a statistical summary of a series of *effects* going on across the population in the lives of individual organisms. Based on his view, the 'direct cause' criterion is too strong, because it excludes selection itself from any list of basic evolutionary processes.

Even if we disagreed with these arguments derived from Walsh, and attempted to hold onto the view that the genuine evolutionary processes are those that involve 'direct' changes of trait frequency change, it would be hard to see what would enable the asymmetrical verdict that selection is a 'direct' cause, but niche-construction is not. The mode of construction of a beaver's dam determines the beaver's success in avoiding predation, and hence in producing offspring: this is a case of niche-construction. The speed of maturation determines the onset of an organism's first brood, and hence overall reproductive output: this is a case of natural selection. Suppose we argue that natural selection is a 'direct' cause of trait frequency change in the speedy maturation example, simply on the grounds that 'selection' names a set of causal processes that make the population change its constitution. Based on this sort of view, niche-construction is also a direct cause of trait frequency change, because 'niche-construction' also names a set of causal processes that make the constitution of the population likely to change.

Resolving the process debate

Natural selection is typically characterized in a highly abstract way that encompasses all cases where there are fitness differences between variants, including when those differences are the upshots of organisms influencing their environments. This means that niche-construction is often an instance of natural selection, rather than a general evolutionary process to be contrasted with natural selection (often, but not always: the discussion of adaptation in the next section of this paper includes an example where niche-construction is rightly understood as an alternative to selection).

In this section I argue that this does not mean we should side with Scott-Phillips *et al*. (2014) in rejecting talk of niche-construction as an evolutionary process. I do so by drawing on parallels with sexual selection. Fisher (1915) argued for the distinctive character of runaway sexual selection by pointing to a reinforcing feedback mechanism between sexual preference and ornamentation. The form of selection at work is reflected in expected reproductive output, and hence sexual selection is a type of natural selection when the latter is construed in abstract terms (Gayon, 2010). Attempts to deny that niche-construction should count as an evolutionary process, if they simply point to a more abstract encompassing role for natural selection, prove too much. That is because they also show that runaway sexual selection is not an evolutionary process.

In the previous section I argued that whether something is to count as an evolutionary process should not depend on whether it is a 'direct' or 'indirect' cause of change. Nor should it depend on whether it gives us one of the most abstract ways of thinking about how populations change. Instead it depends on the advantages from the point of view of investigation, modelling and so forth of making generalizations that unite a given class of events. Runaway sexual selection counts as an evolutionary process because invoking it allows us to explain, via a specific set of models, the appearance of traits that would otherwise be puzzling.

Futuyma – an accretionist – has likewise pointed out that biologists find it useful to think of kin selection, linkage disequilibrium and Red Queen effects as evolutionary processes. He suggests, in line with the analysis offered here, that there is little to be gained by trying to determine which are 'core' processes. Even so, he immediately adds that, 'none of these seems to be as fundamental and comprehensive as mutation, genetic drift, gene flow and natural selection' (Futuyma, 2017: 4). I have suggested that even if natural selection is more 'fundamental' than sexual selection, in the sense of being a higher-order abstraction that encompasses the latter, it does not follow that we have no good reasons for looking in detail at the specifics of sexual selection, understood as an evolutionary process in its own right. The same, I suggest, goes for niche-construction. We need not squabble over whether it is 'fundamental'. The better question to ask is whether it is important, in the sense that models of niche-construction allow us to shed light on phenomena that would otherwise go unseen, or remain unexplained. This is a deflationary approach to niche-construction, which suggests a form of compromise between EES radicals and accretionists.

Fisherian runaway sexual selection merits being described as an evolutionary process because of the manner in which a set of events linked by positive feedback help to explain why selective pressures that might seem opposed to good health and survival can become entrenched and accentuated over time. EES radicals have argued for a similar justification for drawing sets of events together under the heading of 'niche-construction'. They point to trans-generational feedback cycles between causal influences over environmental features, selection pressures and plastic reactions to environments that are tuned over development time. They argue that these sub-processes can establish selective regimes with greater stability than would be naively expected (Odling-Smee *et al*., 2003; Laland *et al*., 2017). This is not the place to examine these models in detail. My claim is simply that this pragmatic strategy is the right one to use if niche-construction is to be established as an evolutionary process. More precisely, because different forms of niche-construction might be shown, via modelling, to have different characteristic evolutionary effects, we might establish niche-construction as a family of related evolutionary processes.

ADAPTATION

Perhaps the most significant element of the EES debate concerns natural selection and the explanation of adaptation. Accretionists like Charlesworth *et al*. (2017: 10) claim that, 'allele frequency change caused by natural selection is the only credible process underlying the evolution of adaptive organismal traits'. Meanwhile radicals such as Laland *et al*. (2015: 6) are more pluralist: 'the burden of creativity in evolution (i.e. the generation of adaptation) does not rest on selection alone.' One camp says selection is the only process that explains adaptation. The other says there are several.

We will now see that there are comparatively mild and strong interpretations of Laland *et al*.'s claim. Milder readings tell us that there are explanatory questions that relate to adaptation that are not answered by appeal to selection. Stronger readings tell us that there are instances of adaptations that are not the products of selection at all. EES radicals often endorse all of these interpretations.

Enriching explanatory contrasts

As a preliminary to introducing the milder readings of Laland *et al*.'s claim that creativity does not rest solely on selection, it is useful to remember that explanatory questions are typically contrastive (Lipton, 2004). Different contrasts make different responses explanatorily appropriate. If we ask why a famine occurred in Africa rather than in Europe, it might be reasonable to cite drought. If we ask why that same famine occurred in Africa rather than in India, we might need to give a different answer based on effective disaster relief.

Now suppose we are asking questions about peppered moths. If we ask why the melanic form, rather than the lighter form, persists in the woods of Derbyshire (UK), then a good answer appeals to cycles of natural selection acting on genetic variation. But we can also ask why these moths evolved camouflage, rather than shooting noxious chemicals at the birds. It is likely that the right answer will appeal to the far greater developmental accessibility of cryptic phenotypes. These kinds of questions point us in the direction of explanations that show why the range of variation on offer to selection tends to facilitate one adaptive pathway, while closing off others (see Huneman, 2017; Marchini *et al*., 2017). They may sometimes be answered by appeal to developmental processes specific to certain taxa, sometimes by appeal to general thermodynamic properties of organic materials: hence, 'Developmental processes … share with natural selection some responsibility for the direction and rate of evolution' (Laland *et al*., 2015: 2).

Interpreted in this way, Laland *et al*.'s claim that 'the burden of creativity in evolution (i.e. the generation of adaptation) does not rest on selection alone' is compatible with Charlesworth *et al*.'s conviction that natural selection 'underlies' the evolution of all adaptive phenotypes. This comparatively mild interpretation does not deny, for example, that the mutational and phenotypic changes on which selection acts are 'random' with respect to fitness. Instead, it reminds us of the rich range of explanatory questions we can ask about adaptive phenotypes, and of the rich range of resources we may need to turn to in order to answer them. Much of Müller's (2017) case for extension can be understood as a demand for a broader set of explanatory contrasts that we might entertain when we ask why we see the adaptations we do.

EXPLORATORY PROCESSES

There are stronger readings of Laland *et al*.'s contention that the explanation of adaptation outstrips selection. They argue that some elements of adaptive fit between phenotype and environment are not the result of selection acting on gradual variation over several generations: here they come into genuine conflict with accretionists.

Charlesworth *et al*. (2017) explicitly exclude cultural evolution from their discussion of selection and adaptation. Even so, if we consider individual organisms that have the capacity to learn during their lifetimes, then we find uncontroversial examples that illustrate Laland *et al*.'s broader idea. Trial and error learning can enable an individual organism to acquire the capacity to deal with an environmental challenge – perhaps the arrival of a new kind of predator – that has never been encountered by the population in the past. That is to say, the capacity acquired by our focal organism – in this case we imagine it to be the ability to fend off a predator never before encountered by the species in question – need not be the developmental expression of earlier selection for the very same capacity in the past. The individual might then transmit this new-found capacity to its offspring. In this way, a process other than natural selection explains the acquisition of a new adaptive capacity.

The significance of this result should not be exaggerated. Natural selection acting over generations may well explain why organisms of the species in question are able to learn by trial and error in the first place. Selection need not be irrelevant, then, if we are to understand the origin of the underlying capacity that explains how the species we are contemplating becomes able to evade these new predators. Selection may also have equipped the species with various learning heuristics, and even with some innate knowledge regarding predators similar to our novel one. Even so, at least part of the answer to the question, 'How is it that this particular organism, and subsequent individuals influenced by it, were able to evade this new predator?', points to the process of learning as carried out over developmental time. Learning also demonstrates how niche-construction may sometimes constitute a straightforward alternative to selection when it comes to understanding the generation of adaptation: a population colonizing a very cold environment might develop physiological adaptations over time under the influence of selection, or it might learn over a much shorter timespan how to modify its niche – perhaps by building shelters – in ways that compensate for the environmental change (Odling-Smee *et al*., 2003). Hence Futuyma's (2017: 1) claim that, 'Directional or positive natural selection is the *only* known cause of adaptive change' (emphasis added), only has plausibility if he is implicitly excluding developmental processes like trial and error learning from his verdict.

Learning constitutes an illustrative instance of Laland et al.'s (2015: 6) claim that, '… exploratory processes, commonplace throughout development, are powerful agents of phenotype construction, as they enable highly diverse functional responses that need not have been pre-screened by earlier selection'. One question, on which radicals and accretionists disagree, is whether (as accretionists seem willing to concede) learning is the only instance of this general pattern or whether (as radicals claim) there are several other 'exploratory' processes, whereby forms of interactive feedback over developmental timescales allow the creation of functional phenotypes in response to environmental challenges not previously encountered in the population's history.

FACILITATED VARIATION

There is a second aspect of stronger versions of Laland *et al*.'s contention that selection does not provide the whole story about adaptation. They claim that the phenomenon of 'facilitated variation' helps to explain how 'functional responses' – i.e. fitness-enhancing responses – can be produced that 'need not have been pre-screened by earlier selection' (see Gerhart & Kirschner, 2007). An elegant form of this type of explanation can be found in work by Richard Watson and collaborators.

At the risk of creating confusion, our discussion now turns away from learning as it occurs over the life of an individual, and towards learning understood as a source of analogy for how we think of selection across multiple generations. It is commonplace to note that developmental processes can be modified by natural selection as the gene networks that influence those processes evolve. Watson *et al*.'s (2014) novel insights are based on their contention that 'gene networks evolve like neural networks learn'. This allows them to apply general lessons from learning theory, derived from theoretical and simulational work on neural networks, to evolution by natural selection. In a series of publications (e.g. Watson *et al*., 2014, 2016; Watson & Szathmary, 2016; Kouvaris *et al*., 2017), these researchers have used these insights to show why we should expect the phenotypic variation available to selection to be more likely to enhance function than we might naively think, even when environmental challenges are presented that the lineage has not been exposed to in the past.

Watson and collaborators argue that selection acting over multiple generations on gene networks is formally equivalent to a learning process in a neural network. This has significant impact on how we understand what selection can achieve. They conclude that, 'the possibility that evolution can learn from experience to favourably bias future exploration need not be any more mysterious than the basic result that learning from a training set can produce good generalisation on an unseen test set' (Watson & Szathmary, 2016: 152).

In what sense does this form of research challenge the contention of accretionists like Futuyma or Charlesworth *et al*. who, to repeat the latter's credo, hold that 'allele frequency change caused by natural selection is the only credible process underlying the evolution of adaptive organismal traits' (Charlesworth *et al*., 2017: 10)? There is no suggestion in these elements of Watson's work that a hitherto unrecognized process must be added to evolution by natural selection, which supplements or replaces selection in the explanation of adaptation. (In work that is not yet published, but which was presented at the Evolution Evolving conference in Cambridge, April 2019, Watson has made a case for a process he calls 'natural induction', which potentially offers a far more significant challenge to the claim that all adaptation is explained by cycles of selection.)

Instead, we simply have more cycles of mutation and reproduction, with some variants contributing more to future generations than others. Far from Watson and collaborators framing these articles as a challenge to selection's ability to explain complex adaptations, they instead see their work as showing precisely how selection is able to explain such adaptations. In their view, learning models offer, 'the potential to better explain how the process of random variation and selection results in the apparently intelligent designs it produces.' (Watson & Szathmary, 2016: 155).

It would be a mistake, though, to suggest that this type of work leaves our basic understanding of the explanation of adaptation untouched. Watson and collaborators take themselves to have shown that selection processes have a series of capacities that have not been well understood: 'evolution can learn in more sophisticated ways than previously realised' (Watson & Szathmary, 2016: 147). They are quite right to say that, 'In current evolutionary theory, it seems impossible that natural selection can anticipate what is needed in novel selective environments' (Watson & Szathmary, 2016: 155); and yet, their use of learning theory gives a precise account of the circumstances under which a very specific form of anticipation can occur. Accretionists may feel comforted that selection, in these pieces of work at least, retains a privileged position with respect to the explanation of adaptation. Radicals should also be encouraged by the significant challenge to the familiar affordances with which selection processes have been credited.

CROSS-CUTTING VERDICTS ON THE EES

The most basic point this article has established concerns the exceptionally wide range of issues in play in the context of debates over the EES. There are at least three levels to be discerned.

First, and most obviously, there are fairly clearly defined first-order empirical issues. One example concerns the extent to which forms of non-genetic inheritance are trans-generationally stable and widely distributed across many taxa. Second, the questions often concern historical matters. Here the topics under discussion include whether the MS is best understood as a series of assumptions or hypotheses that might be shown true or false; whether it is better understood as a malleable set of investigative tools, or a loose alliance of diverse researchers; and whether the mainstream of work in evolutionary theory has shown inflexible constraining tendencies, or whether it has instead shown forms of adaptive plasticity in the face of new problems, new data and new techniques. Third, the issues at stake are often of a philosophical/conceptual nature. A selection of such questions includes what it takes for something to be an 'evolutionary process'; whether natural selection is the sole explanation of adaptive phenomena; and whether evolutionary theory needs to abandon a 'linear' conception of biological causation – exemplified by the notion that selection is a unidirectional force that moves from environment to organism – and should instead adopt a 'reciprocal' understanding of causation in terms of various forms of feedback and mutual determination.

In pulling out these three dimensions of the EES debate, I do not mean to imply that they are independent of each other: indeed, we have seen clearly that they are not. What might seem to be an empirical question about the nature of epigenetic inheritance, for example, takes on a conceptual dimension when we ask what its significance is for evolutionary change. Are we assuming that such an inheritance system must have similar properties to the genetic inheritance system, or should we instead consider how systems that are not able to perpetuate the inheritance of differences over many generations might be able to influence the evolutionary fate of a population in alternative ways? Our discussion of Fisher on sexual selection reminds us that what might seem to be a predominantly conceptual question about the nature of evolutionary processes takes on a historical dimension when we ask to what degree the EES radicals' understanding of processes truly marks a break from what has gone before, in terms of how selection itself is understood.

I do not mean to imply that Laland, Müller, Uller, Pigliucci, Futuyma or other key actors in these debates would be surprised to learn that there are conceptual and historical foci of dispute in these debates: indeed, it has been a self-evident theme in their own work. What, then, is the value of noting the diversity of themes under discussion in the specific ways highlighted here? It helps to illuminate the many cross-cutting assessments a well-informed biologist might come to when asked to reach a verdict on the EES, and thereby explains why that debate is so hard to resolve. Here is a subset:

- One might enthusiastically endorse the significance of non-genetic inheritance for modifying evolutionary dynamics, while adding that formal approaches using the Price equation give us useful tools for understanding these influences. Here one might be a radical at the level of evolutionary hypotheses, but an accretionist at the level of analytical tools.
- One might deny the significance of non-genetic inheritance for evolution, while using Watson's work to argue that evolutionary theorists have not fully appreciated the capacity of selection to produce systems with a significant ability to anticipate novel environmental challenges. Here one might be accretionist when it comes to the hypothesis that natural selection accounts for adaptation, while being more radical when it comes to the sorts of tools we need to use to understand selection's capacities.
- One might argue that niche-construction generates important forms of stabilized adaptive trajectories that have not been properly appreciated. Even so, one might deny that this makes a case for placing a new notion of 'reciprocal causation' at the centre of evolutionary theory. One might claim that reciprocal causation has been in the mainstream of evolutionary thinking – in models of runaway sexual selection, for example – for over 100 years.

WHAT WOULD SUCCESS LOOK LIKE FOR THE EXTENDERS?

There are further insights that our atomization of the EES offers. Once we note how elements of radical and accretionist positions can be combined in many ways, we also highlight a series of complexities when it comes to spelling out what success for EES radicals would look like.

It is possible to imagine a future in which the textbooks that have been used in multiple editions for the past 40 years are significantly rewritten. Perhaps they will give selection a less prominent role in the explanation of adaptation; they might introduce a whole series of important modes of inheritance alongside genes; they might consider changes to gene frequencies merely as a rather special case of a far more general phenomenon of evolutionary change over time; and they might place considerable stress on reciprocal causal interactions between processes of development, inheritance and selection. Were this to happen, it would constitute a signal that a root-and-branch overhaul of evolutionary theorizing had occurred.

Some advocates of the EES may view success in such terms. Müller, for example, notes a series of 'empirical and conceptual advances' in the understanding of several different evolutionary phenomena, and remarks that it would be surprising if, 'in the midst of a substantial growth of knowledge, the central theory uniting the different fields of biology remained unaltered' (Müller, 2017: 1). Müller's view is that this central theory should be urgently reworked.

The range of issues under discussion indicates how hard it will be to secure a victory of this ambitious sort. The radicals' positions only receive full endorsement when one is willing to agree to many different claims. A small selection include: their empirical assessments of epigenetic inheritance; their historiographical stance regarding the nature of the MS and its constraining role; and their philosophical positions regarding the status of natural selection, the general features of evolutionary processes, and the need to place reciprocal causation at the centre of a re-engineered synthesis. This is not all: I have been silent in this article on a series of further questions including the notions of genetic accommodation and 'genes as followers', the value of the proximate/ultimate distinction, and the very definition of evolution in terms of changing gene frequencies. As a purely tactical matter, it is difficult to convert individuals to a position which, in its full-blooded form, demands assent to so many different contested claims, at so many different levels of analysis.

It is worth considering, then, a different outcome that would still signal a strong vindication of many sub-themes stressed by advocates of the EES. Imagine that a moderately sized community of biological researchers emerges who are explicitly inspired by something they jointly call the 'Extended Evolutionary Synthesis'. (This appears to be what is happening right now as a result of research sparked by Laland, Uller, Müller and the many other collaborators they have worked with.) They take an interest in each other's work. They regularly produce pieces of empirical and theoretical research that all evolutionary thinkers – including those who continue to work within the mainstream – acknowledge to be of value. These pieces of ground-level research (as opposed to high-level reflections on the general structure of evolutionary theory) might cover wide domains of enquiry. They might use the Price equation to show how forms of inheritance interact. They might demonstrate specific ways in which animal choices influence evolutionary trajectories. They might uncover new forms of exploratory adaptive feedback, akin to learning, that take place during development. They might offer detailed models of specific developmental processes, and the ways they affect adaptive pathways followed and not followed. They might yield increased understanding of the precise circumstances under which we can expect genetic variation to anticipate environmental change.

I have suggested in this paper that there is considerable diversity – even disunity – in the themes explored by EES radicals. It might seem that this amounts to an argument for abandoning all talk of the EES as such, in favour of more focused attention on a series of more tractable, lower-level questions about developmental bias, epigenetic inheritance, exploratory developmental processes and so forth. I showed the attractions of such a deflationary conclusion when examining the niche-construction debate. There, I recommended a pragmatic account that recognizes a plurality of overlapping evolutionary 'processes' – natural selection, runaway sexual selection, various forms of niche-construction – whenever we have models that illuminate evolutionary questions in novel ways.

If we allowed this deflationary view to eliminate all talk of the EES we would, however, have gone too far. The EES becomes more than a mere collection of researchers driving valuable work on diverse sub-topics, and instead earns its keep as an integrated programme of investigation, when insights from different themes are brought together to inform each other. This can happen when researchers start to draw links between work on developmental plasticity and niche-construction (e.g. Moczek, 2015); when they conjecture interactions between work on various forms of developmental bias and evolvability (e.g. Uller *et al.*, 2018; Duckworth *et al.*, 2018; Badyaev *et al.*, 2019); when they explore the links between evolutionary rationales for adaptive plasticity and the origins of forms of non-genetic inheritance (e.g. English *et al.*, 2015); and when they use insights from connectionist models of learning to shed light on mutual interactions between the capacities of selection and the organization of the systems that comprise evolving populations (e.g. Watson *et al.*, 2016). Even when this happens, the very malleability of the tools we use for evolutionary enquiry offers accretionists multiple ways to accommodate – and even to co-opt – insights and approaches generated by those working under the banner of the EES. These are victories for the EES as such, for they are victories that are the distinctive product of a coming-together of researchers working on the themes stressed by EES enthusiasts. But they are victories that can be celebrated by all evolutionists.

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