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Introduction

Evolutionary accounts of human behavioural diversity

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Human beings persist in an extraordinary range of ecological settings, in the process exhibiting enormous behavioural diversity, both within and between populations. People vary in their social, mating and parental behaviour and have diverse and elaborate beliefs, traditions, norms and institutions. The aim of this theme issue is to ask whether, and how, evolutionary theory can help us to understand this diversity. In this introductory article, we provide a background to the debate surrounding how best to understand behavioural diversity using evolutionary models of human behaviour. In particular, we examine how diversity has been viewed by the main subdisciplines within the human evolutionary behavioural sciences, focusing in particular on the human behavioural ecology, evolutionary psychology and cultural evolution approaches. In addition to differences in focus and methodology, these subdisciplines have traditionally varied in the emphasis placed on human universals, ecological factors and socially learned behaviour, and on how they have addressed the issue of genetic variation. We reaffirm that evolutionary theory provides an essential framework for understanding behavioural diversity within and between human populations, but argue that greater integration between the subfields is critical to developing a satisfactory understanding of diversity.

Keywords: diversity; behaviour; human beings; evolution; cognition; culture

1. INTRODUCTION

Human beings exhibit a large amount of behavioural diversity both between and within populations. Between populations, some behavioural characteristics are observed in some populations and not others; such traits might include driving cars or graduating from college. Other traits, such as eating and speaking, are found in all populations, but exhibit variation in their expression, for example, in the type of food eaten and the language spoken. In other cases, behaviour varies within populations, with individuals of different ages, sexes, vocation and social status being involved in different activities and having different roles, rights and responsibilities. Behaviour also varies within individuals over the course of their lifetimes, and stable individual differences extend beyond that which can be attributed to differences between populations or subgroups. In this article, we use the term *diversity* to apply broadly to all of these aspects of behavioural variation. Thus, we define *behavioural diversity* as

encompassing the different and varied behaviour patterns exhibited by human beings, both between and within populations, and the variation exhibited within and between individuals. This definition is purposefully broad, as our aim is to assess whether evolutionary theory can help us to understand any or all of these aspects of human behavioural diversity.

Within academia, human behavioural diversity has been the focus of social and cultural anthropological research for over a century [1]. In addition, psychology has had a longstanding interest in the causes of individual differences [2]. However, these disciplines have generally not incorporated advances in evolutionary biology into their accounts of behavioural diversity. We begin the article with a brief overview of the historical debate surrounding the application of evolutionary theory to human behaviour, in order to show how the current field of human evolutionary behavioural sciences has arisen. We then focus on the three prominent subdisciplines that have emerged, namely human behavioural ecology, evolutionary psychology and cultural evolution. While these subdisciplines share the assumption that evolutionary theory can usefully be applied to the study of human behaviour, researchers from these different perspectives

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One contribution of 14 to a Theme Issue 'Evolution and human behavioural diversity'.

have disagreed on non-trivial points [3–5], such as the extent to which genes, environments and socially transmitted information explain behavioural variation. We set ourselves the objective of isolating the key points of contention, and considering how differences of opinion might be resolved. We believe that a genuine understanding of human behavioural diversity can only come from an integration of the subfields [3,4].

The contributors to this issue are researchers who have embraced a cross-disciplinary or integrative perspective on human behaviour. The impetus for the issue was the formation of the European Human Behaviour and Evolution Association (EHBEA) in 2008 and its inaugural annual conference, which was held at the University of St Andrews, UK, on 6–8th April 2009. EHBEA is an interdisciplinary academic society that supports the activities of European researchers in the human evolutionary behavioural sciences and that explicitly endeavours to promote pluralism and integration within the field.

2. ASKING QUESTIONS ABOUT BEHAVIOUR

The ethologist Niko Tinbergen [6] outlined the fact that, when we ask why an animal exhibits a particular behaviour pattern, we could potentially be asking one of four different questions. First, we can ask questions about the *function* of the behaviour pattern, by which is meant the role that the trait plays in enhancing reproductive success. Second, we can ask about the *evolutionary history* of the behaviour pattern, including an account of its original ancestral state and the selective pressures in the evolutionary history of the lineage that led to the species possessing this derived behaviour. Third, we can ask what *proximate* causes lead the individual to express the behaviour pattern, for instance, by looking at the sensory input, neural mechanisms and effector systems that produce behaviour. Finally, we can ask what factors during *development* have played a role in directing the appearance of the behaviour at the relevant stage in its lifetime. For each of the subfields of the human evolutionary behavioural sciences (human behavioural ecology, evolutionary psychology and cultural evolution), we assess which of these questions researchers prioritise when examining human behavioural diversity. However, we begin by examining how these subfields have arisen historically. This historical perspective should provide the reader with a deeper understanding of how the differences of opinion that exist among contemporary approaches have arisen (for a more extensive account, see [3]).

During the 1950s, the primary group of researchers studying animal behaviour was the ethologists, who focused on proximate mechanisms asking, for example, which stimuli in the environment elicited relatively fixed behavioural responses. The ethologists also explored the evolutionary history of characters, by using the methods of comparative anatomy to examine the differences in species-typical behaviour patterns between closely related species [7,8]. A focus on development and role of individual experience was only fully incorporated into the discipline following robust critiques from the comparative

psychologists [9]. While the ethologists started with the assumption that behaviour patterns function to enhance survival or reproductive success, and while Tinbergen pioneered the study of function of behaviour through elegant field experimentation, it was really causation that was the ethologists' primary focus [8]. In practice, the study of function only came to the fore during the 1960s and 1970s, through the ground-breaking research of evolutionary biologists, such as William Hamilton, Robert Trivers, John Maynard Smith and George Williams. The theoretical advances of these researchers paved the way for a new understanding of animal behaviour that took a gene's-eye perspective [10,11]. Behaviour patterns such as aggression, cooperation and parenting were being evaluated in terms of the relative reproductive success of different strategies, and the notion that animals behaved 'for the good of the group or the species' was rejected. This did not mean that cooperative behaviour patterns and reciprocal exchanges could not evolve, but rather that such behaviour was explained in terms of the fitness advantages to individual genotypes. The gene's-eye view was to revolutionize the study of animal behaviour.

Harvard biologist Edward Wilson applied this reasoning from evolutionary biology to human behaviour. In the concluding chapter of *Sociobiology: the New Synthesis*, he offered bold, and often speculative, explanations for such controversial topics as sex roles, homosexuality, aggression and religion [12]. Wilson's critics immediately charged him with prejudicial story-telling and genetic determinism [13,14]. While, according to Wilson, all individuals are undoubtedly influenced by their physical environment, and social or cultural, environment, Wilson's sociobiology was in the nativist tradition that emphasized the strong influence of a genetic inheritance on behaviour. He was a stalwart proponent of the idea that universal human nature can be described and scientifically investigated [15]. For Wilson, behavioural diversity could be explained by genetic variation, reflecting a history of differential selection and adaptations for different behaviour in different subgroups, such as men and women.

Wilson's position contrasted starkly with the predominant view of human behaviour within the social sciences, which emphasized the role of socially transmitted information in producing different traditions, beliefs and norms across populations [1]. We have attempted to capture the distinctiveness of alternative perspectives in figure 1, which shows the two inheritance systems in human populations, namely the genetic inheritance that is transmitted from one generation to the next and the socially transmitted information that is present in the population at the first and second time-point, representing successive generations. In figure 1, G represents the gene-pool of the population, and P represents the behavioural phenotype of the population. In the standard social science model, the two inheritance systems (represented by the arrows) are viewed as quasi-independent, with little interaction between them (figure 1a). The legacy of genetic inheritance is assumed to provide human beings with a mind capable of learning, but

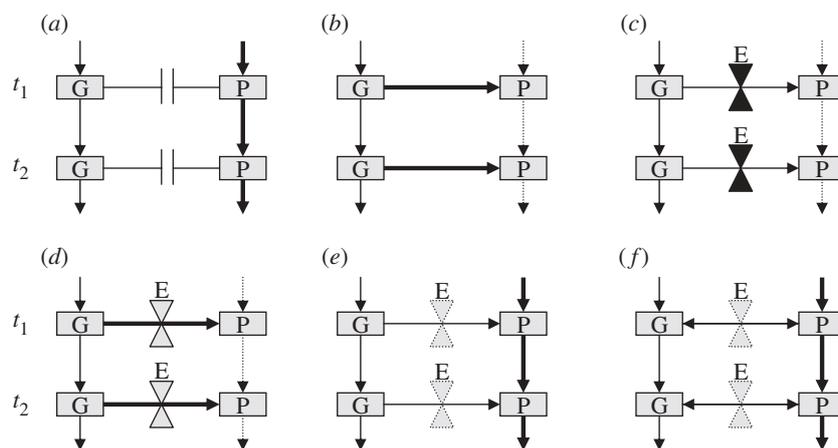


Figure 1. Summary of how the standard social science model and the subfields of the human evolutionary behavioural sciences view human behaviour. The two inheritance systems in human populations, namely, the genetic inheritance that is transmitted from one generation to the next (G) and the socially transmitted information that is present in the population at the first and second time-point, and potentially shapes the phenotype (P), are represented for two successive generations (t_1 and t_2). (a) The standard social science model stresses the strong influence of socially transmitted information on behaviour (thick arrows from P to P) and the lack of interaction between the two inheritance systems (broken lines between G and P). (b) Human sociobiology stresses the impact of genetic inheritance on human behaviour (thick arrows from G to P) and the relatively weak influence of socially transmitted information (thin arrows from P to P). (c) Human behavioural ecology stresses the role of the environment (E) in modulating behavioural development and eliciting alternative behaviour patterns, while still acknowledging the existence of two inheritance pathways. (d) Evolutionary psychology stresses the impact of genetic inheritance on human behaviour (thick arrows from G to P), the relatively weak influences of socially transmitted information (thin arrows from P to P), and the role of the environment (E) in eliciting alternative behavioural responses. (e) Cultural evolution theory stresses the role of socially transmitted information in human behaviour (thick arrows from P to P), while still acknowledging some role for genetic inheritance and environmental input. (f) Gene–culture coevolution stresses the role of both genetic and socially transmitted inheritance, the interactions between the two inheritance systems (two-way arrows between G and P, which are also described by niche construction theory), and the role of the environment on these interactions.

the behaviour exhibited by individuals is thought to be largely shaped by socially transmitted information. In comparison, Wilson's human sociobiology placed stronger emphasis on the genetic influences on human behavioural phenotype (represented by the dark arrows from G to P), and he described genes as 'holding culture on a leash' ([15, p. 172]; figure 1b).

While the primary emphasis of human sociobiology was on the role of genetic inheritance in producing a universal human nature and explaining variation between subgroups, the physical and cultural environments were not rejected out-right as sources of influence. For example, Richard Alexander [16] discussed how the physical environment could prompt adaptive responses, and thereby explained behavioural variation as plastic responses to varying conditions. Alexander's focus on adaptive phenotypic plasticity strongly influenced the emerging field of human behavioural ecology. Subsequently, some evolutionarily minded psychologists took up the argument that the human mind contains in-built, evolved structure that gives rise to universal human nature [17]. For example, Donald Brown [18] outlined the behavioural traits that are apparently shared across all human populations. Some biologists stressed the potency of socially learned information on human behaviour; for instance, Richard Dawkins [10] put forward the idea of memetic evolution, while Charles Lumsden & Edward Wilson [19] examined how genes and socially transmitted information might interact over evolutionary timeframes. These developments helped to prompt

the emergence of cultural evolution theory, although early advocates of this field were frequently critical of aspects of sociobiology [20,21]. From these beginnings, three main subfields have emerged that constitute the contemporary field of human evolutionary behavioural sciences. In the following section, we emphasize the historical or traditional perspective of each community, an approach that inevitably fails to capture recent initiatives within the fields. While we acknowledge that some researchers have adopted theoretical positions and methodological techniques from more than one of the subfields and do not align themselves with a specific approach, we (and others) have argued previously that characterizing the field as containing boundaries is a useful and a valid perspective [3–5,22]. In a later section, we consider to what extent the different subfields have changed in recent years and whether these approaches should be considered complementary or contradictory, and we provide examples of cross-disciplinary, integrative research that has examined human behavioural diversity.

3. THE HUMAN EVOLUTIONARY BEHAVIOURAL SCIENCES

(a) *Human behavioural ecology*

During the 1970s, a small field emerged within anthropology that has become known as human behavioural ecology. Early proponents of this field, notably Richard Alexander, Irven DeVore, William Irons and Napoleon Chagnon, attempted to explain

human behaviour based on the assumption that individuals behave in a manner that maximizes their reproductive success [23,24]. These anthropologists applied the optimality models and analyses that had been developed by Eric Charnov, David Lack and others to ask questions about human behaviour. For example, human behavioural ecologists have investigated whether human beings hunt in optimal group sizes [25], whether marriage choices follow the polygyny threshold model [26] and whether inter-birth intervals maximize reproductive success [27]. A key assumption of the field is that human behaviour is highly flexible and is likely to produce adaptive outcomes in response to specific environmental parameters.

Human behavioural ecologists use mathematical models taken from evolutionary biology and ecology to make predictions about the behaviour of individuals. These researchers assume that behaviour will be adaptive in the sense of increasing an individual's reproductive success, rather than simply functioning to serve the individual's immediate needs. For the behavioural ecologist, variation in human behaviour largely reflects adaptive responses to variation in the environments encountered. While human behavioural ecologists focus on behavioural diversity within populations, their research is based on the theoretical assumption that between-population behavioural diversity will be seen, as different environments will be predicted to produce different adaptive behaviour patterns. Thus, human behavioural ecology places emphasis on the role of the environment (E) in eliciting the optimal, and therefore most frequently expressed, behavioural phenotypes (figure 1c), without extensive discussion of whether genes, socially learned information or other factors, are responsible for the apparent match between phenotype and environment [22]. Indeed, in this respect, the behavioural ecologists can be portrayed as mechanism-neutral. This stance does not equate with the idea that human beings are infinitely flexible, as human behavioural ecologists assume that constraints in the underlying genetic or neural mechanism will limit the range of environmental conditions in which adaptive responses will be produced.

Far from lamenting the fact that their approach pays little attention to proximate mechanisms, many human behavioural ecologists regard this as a virtue. Human behavioural ecologists have been viewed as documenting the range of possible strategies that can be produced by universal cognitive mechanisms [28]. A history of natural selection is assumed to have endowed our species with the ability to weigh up the costs and benefits of adopting particular strategies, and it is these decision rules (and the underlying cognitive and physiological machinery behind them) that are assumed to have been the focus of selection [29]. By avoiding answering questions about mechanisms, human behavioural ecologists' adherence to the *phenotypic gambit* [30], which posits that the constraints on decision rules, be they genetic, psychological or social, are so minimal as to justify their being ignored in the construction of models and the testing of hypotheses. For many human behavioural ecologists,

it simply does not matter whether humans end up behaving in an adaptive manner as a consequence of their psychological mechanisms, their learning or their culture. As long as their behaviour is adaptive, then it can be predicted with formal models. For these researchers, the key legacy of our evolutionary history is *adaptability* not psychological or behavioural adaptations. This adaptability may itself be an adaptation, albeit an extremely general one.

(b) *Evolutionary psychology*

At the beginning of the twentieth century, psychology was dominated by the behaviourists, who viewed the brain largely as a *tabula rasa*, with no centrally initiated processes other than a general ability to learn [31,32]. However, the cognitive revolution within psychology during the 1950s and 1960s revitalized the idea that the brain is not blank at birth [33]. Animal behaviour researchers were showing that some associations are learned more easily than others [34], presumably because of constraints or biases in the underlying neural system. Such research implied that a general-purpose learning system could not adequately account for all behaviour, and that individuals possess evolved psychological mechanisms. At the same time that human behavioural ecology was emerging as a discipline, the application of evolutionary perspectives to human psychology was gaining critical momentum. Particularly important in this revival were Leda Cosmides, John Tooby and Donald Symons. These researchers argued that evolutionary theory could be applied to the study of how the mind works and could individuate evolved psychological mechanisms that underlie universal human traits. Cosmides and Tooby promoted the idea that the human brain consists of specialized psychological mechanisms that have evolved in response to selection pressures acting on our ancestors, particularly during the Pleistocene [17]. Evolutionary psychologists have posited evolutionary explanations for a broad range of domain-specific mechanisms, including sexual jealousy, aggression, social exchange and morality [35].

While some evolutionary psychologists eschew any historical links with human sociobiology [17,36], in many respects, evolutionary psychologists view the major sources of influence on the human behavioural phenotype in a very similar manner to the human sociobiologists that preceded them. Like sociobiology, evolutionary psychology has placed considerable emphasis on the role of genes in underpinning a universal human nature (figure 1d). Evolved psychological mechanisms are assumed to process environmental inputs, such that particular inputs will flip these mechanisms into one of a number of states, thereafter eliciting appropriate behavioural outputs. In so doing, the organism is adaptive as a consequence of its underlying adapted mechanisms, and the number of possible switches that a mechanism has marks the evolved parameters of that mechanism. The ability of inputs to shift the behavioural output of this universal genetic programme in an adaptive, context specific manner, has been described as analogous to how the buttons of a jukebox change the tunes

it plays [37,38]. Behavioural diversity, both within and between cultures, can therefore result from the expression of pre-existing behavioural variants, each of which can be viewed as the pre-specified outputs of adaptive programmes that have been fashioned by natural selection [39].

Prominent evolutionary psychologists have argued that culture can be divided into three categories: universal, evoked and epidemiological culture [38,40]. ‘Universal culture’ refers to human nature: the sort of traits outlined by Wilson [12,15] and Brown [18] as universal to all human populations and underlain by our evolved psychological mechanisms. This category of culture is represented in figure 1*d* by the large arrow portraying genetic influences on behaviour (thick arrows from G to P). ‘Evoked culture’ is the subset of culture that is evoked by the local environment and, as long as the environment is not too different from that experienced by our ancestors, will produce an adaptive fit (as emphasized and indeed measured by human behavioural ecologists). In figure 1*d*, this is captured by the environmental modulator (E) acting on the genetic influence on the human behavioural phenotype. ‘Epidemiological culture’ refers to those aspects of culture that are socially transmitted between individuals and that can vary rapidly over time (dashed arrows). This type of culture is typically viewed by evolutionary psychologists as having little impact on the evolutionary brain mechanisms that underlie behaviour [38]. While evolutionary psychology therefore does not deny a role for socially transmitted information in shaping an individual’s behavioural phenotype [41], it is assumed to have little causal role in our evolution [42].

(c) Cultural evolution

Edward Tylor [43] and other early anthropologists attempted to rank cultures along a continuum from the most primitive to the most advanced and to describe the stages through which cultures progress. While this progressive notion of cultural evolution does not receive support within the modern academic field of anthropology (although see [44]), the idea that cultural practices change over time, and that the change in the frequency of different cultural variants can be modelled mathematically, has produced a scientific field of research that spans biology and anthropology. The originators of mathematical approaches to the study of human culture include geneticists Marc Feldman & Luca Cavalli-Sforza [21,45] and biological anthropologists Robert Boyd & Peter Richerson [20,46]. These researchers argue that culture can be conceptualized as comprising socially learned information, expressed in behaviour and artefacts (or ‘traits’). Cultural traits may compete with each other, in a similar way to competing alleles or genotypes, and can be studied using models and methods adapted from evolutionary theory. This perspective on culture does not lead to the conclusion that some cultures are more advanced or superior to others, but helps to explain and predict this pattern of cultural change and diversity.

Modern cultural evolution theory emphasizes the role of differential social learning in producing human behavioural diversity, while paying comparatively little attention to the role of genes and environment as direct sources of behavioural variation (figure 1*e*). Nonetheless, there is a broad expectation that cultural traits will frequently be adaptive, since culture is viewed as a means by which humans adjust their behaviour to the environment, and the utility of cultural variants will depend, in part, on the ecological context. Evolved psychological mechanisms are recognized, but the focus tends to be on rather general learning rules (i.e. ‘conform to the majority behaviour’ or ‘copy the most successful individual’). However, for the cultural evolutionist, weak genetic and environmental influences allow cultural transmission to do more than bias the acquisition of pre-specified behavioural outputs: transmitted culture introduces behavioural variants, including entirely novel variants, into the individual’s repertoire. In this respect, the cultural evolutionist school resembles the traditional social science model, in adhering to a strong influence of social learning as a source of behavioural variation. Moreover, for the cultural evolutionist, the cultural change is itself regarded as an evolutionary process, in which cultural traits are devised, spread according to their utility, attractiveness and compatibility with existing traits, and diversify through a cumulative process of elaboration and refinement. This reinforces the perceived role of socially transmitted information as a major source of human behavioural variation.

From the cultural evolutionist’s perspective, the view that social learning can propagate novel behaviour through human populations allows for the possibility that human cultural practices might modify the pattern or strength of selection acting back on the human genome, triggering culture-initiated and population-specific bouts of natural selection, including selection on parts of the genome that are expressed in neural functioning and behavioural responses. Such evolutionary interactions between genes and culture are the specific focus of the field of gene–culture coevolution (figure 1*f*). Gene–culture coevolution can either be viewed as a sub-branch of cultural evolution theory [20] or as a distinct field in its own right [3,47]. From the gene–culture perspective, genes and socially transmitted information are two major inheritance systems that flow down the generations and that interact: an individual’s genotype affects how and what an individual learns, and which cultural traits it adopts, while social information transmission feeds back to modify the selection acting on the population. While perhaps the best known example of gene–culture coevolution is the link between dairy farming and genes for absorbing lactose in milk [48–50], this is far from an isolated example, and gene–culture coevolution may explain within- and between-population variation in numerous genes, including some underlying brain function [51]. The gene–culture perspective, therefore, diverges from the view that socially transmitted, epidemiological culture has little impact on the brain mechanisms that underlie behaviour [38,42].

4. INTEGRATING EVOLUTIONARY PERSPECTIVES ON HUMAN BEHAVIOUR

Having reviewed how the different evolutionary schools explain human behavioural diversity, we now consider to what extent these accounts are compatible. A key question that remains to be fully answered is whether, and how, the concept of a universal human nature might be combined with the large-scale behavioural flexibility and diversity that is observable between and within human populations [42].

(a) *Are there any points of contention?*

While, historically, practitioners of the various evolutionary schools have not always seen eye to eye (e.g. [52–54]), it is important not to assume that there are inevitable and inherent points of contention. Any past disagreements could reflect misunderstandings, personality clashes, methodological differences or outdated perspectives that no longer apply in the contemporary intellectual climate [4]. After all, all of the aforementioned evolutionary perspectives recognize, at some level, three major sources of variation that underpin human behavioural diversity: namely, genetic, environmental and socially learned differences (as well as some interactions between these). While proponents of the different schools may place differing degrees of emphasis on these sources of variation [22], it is natural for any academic field to encompass a range of views over the relative importance of key processes.

Moreover, we have described historical schools, but the contemporary evolutionist is not tied to any one of these approaches and is free to draw from the methods available across the broader field of human behaviour and evolution. Recent edited volumes have spanned these historical lines [35,55–57] and, from this viewpoint, there is apparently little inherent conflict within the human evolutionary behavioural sciences. Evolutionary psychology and human behavioural ecology have been argued to be relatively easy to reconcile, as they merely differentially weight genetic predispositions and environmental sources of variation [28], and both appear comfortable with a weaker role for socially learned sources of variation. As long as cultural evolutionists are viewed as studying ‘epidemiological culture’, and as long as this is perceived to have relatively little influence on evolved psychological mechanisms, all three research traditions might be viewed as being in harmony, with each contributing some understanding to different aspects of human behaviour.

However, other researchers do not see the field in that way and have highlighted key differences central to each subfield [3–5,58]. For example, the gene–culture coevolutionary perspective presents a version of culture that is not easily reconciled with the views proposed by the other subfields. Before discussing the remaining points of contention, we will provide examples of research on behavioural diversity that have drawn methodology or theory from more than one of the subfields described above. We will examine how successfully the subfields have been integrated by researchers taking an evolutionary approach to

behavioural diversity. The most probable topics that could present barriers to a full evolutionary account of human behaviour include acceptance of the role that genes play in diversity, the role of the environment in behavioural development and the importance of transmitted information as a part-cause, not simply a product, of human evolutionary processes.

(b) *Examples of integration*

Several researchers have considered how the human behavioural ecology and evolutionary psychology perspectives could be integrated to provide a new perspective on behavioural diversity (e.g. [39,59–62]). For example, when discussing early onset of female reproduction, Nettle [63] suggests that cost–benefit analyses can predict the circumstances of teenage motherhood. Engaging in early childbearing correlates with early puberty and with relatively low parental investment during early life, suggesting a developmental flexibility that is calibrated by cues in the environment [63,64]. Other researchers have added the idea that individuals might be differentially susceptible to environmental influences, perhaps owing to temperamental or genetic differences [65]. By integrating information about life history, cognitive processing and development, these researchers are attempting to provide a complete understanding of one important aspect of human behavioural diversity (see [61] for another example).

As mentioned earlier, the apparent ease with which evolutionary psychology and human behavioural ecology can be reconciled with each other could result from the idea that the two subfields are asking different, complementary questions about human behaviour [3,4,28,56,66]. Human behavioural ecology attempts to model the outcomes of evolved psychological mechanisms in terms of behaviour and life histories, while evolutionary psychology aspires to map the parameters of these mechanisms within the brain [28]. In terms of Tinbergen’s four questions, human behavioural ecology and evolutionary psychology derive functional hypotheses, while evolutionary psychology also uses evolutionary history to derive hypotheses about *proximate mechanisms* (for critiques of whether evolutionary psychology addresses evolutionary history, see [67,68]). In recent years, evolutionary and developmental psychologists have also used evolutionary theory to derive hypotheses about behavioural development (e.g. [69,70]). As a complete understanding of human behavioural diversity requires all four of Tinbergen’s questions to be addressed, behavioural ecology and evolutionary psychology can potentially be viewed as both compatible and complementary. Indeed, from this perspective, one might add the *evolutionary history* perspective provided by comparative statistical methods [71], comparisons with other species [72] and gene–culture coevolution [47]. Collectively, these alternative approaches could provide a comprehensive understanding of behaviour.

The idea that socially transmitted information can be integrated into the human behavioural ecology perspective is well illustrated by Monique Borgerhoff

Mulder & Bret Beheim [73], who show that childhood mortality risk is related to multiple types of inherited wealth. As some of these wealth inheritance patterns have been interpreted as signatures of vertical transmission of socially learned information [71,74], cultural traits associated with child mortality risk may be influenced by cultural inheritance patterns. Typically, such cultural inheritance patterns would be interpreted as simply one mechanism through which our species adapts its behaviour to the local ecology, but this human behavioural ecology perspective also does not necessarily preclude the notion that such cultural inheritance patterns could potentially operate independently of the influences of ecological variables. For example, human behavioural ecologists have successfully applied optimality modelling to recent life-history changes, such as low fertility in post-demographic populations [75], despite the suggestion that post-industrial cultural change has occurred too quickly to avoid a 'mismatch' or 'adaptive lag' between the environment and our evolved behavioural strategies. Incorporating socially learned transmission of information is therefore not inevitably incongruent with the human behavioural ecology perspective [76,77].

The willingness of human behavioural ecologists to engage with cultural evolutionists should not be surprising. Human behavioural ecology was originally conceived as a mechanism-neutral perspective, such that either socially learned information or genetic differences could account for any between-population adaptive fit with the environment [22]. However, some, perhaps most, anthropologists are highly uncomfortable with any role for genes in explaining variation between populations [78], with some exceptions (e.g. [79]). This reticence to include genetic variation as a source of diversity is likely to result, in part, from the racially discriminatory perspectives on human evolution that permeated the early part of the history of anthropology [3]. However, a modern perspective on the role of genes in human behaviour should be carefully distinguished from the misapplication of a hereditarian view of human abilities. The idea that genetic variation might partially explain within-population differences between individuals in behaviour and cognition has been the focus of human behavioural genetics for several decades [80], and individual genetic variation has partly been incorporated into the evolutionary psychology research framework (e.g. [81–85]).

More controversial is the idea that between-population differences in genetic complement underlie a portion of cross-cultural variation in behaviour. While the extent of genetic variation between populations has been shown to be relatively small compared with the genetic variation within populations [86], and cross-population migrations and matings serve to dilute potential boundaries between gene pools, these arguments do not prove that such genetic differences within and between populations are not meaningful and do not play a role in accounting for some portion of behavioural diversity [67]. Recent analyses of data from the human genome have revealed that numerous genes have experienced recent positive selection, including genes that are

expressed in the brain [87], with considerable selection having occurred in the past 10 000 years [88,89]. Moreover, analyses have shown that recent human evolution is dominated by partial selective sweeps that are specific to particular geographical regions or populations [90]. These data suggest that there are significant genetic differences between human populations that have arisen from recent selective events, with much of the variation fairly broad scale (e.g. continent wide) [91]. While some researchers have acknowledged genetic variation as a potential source of cross-cultural variation in behaviour (e.g. [59,62]), between-population genetic variation has yet to be incorporated fully into the human evolutionary behavioural sciences. The failure to incorporate the findings of human population genetics is a serious inadequacy of the human evolutionary behavioural sciences and currently limits our understanding of behavioural diversity.

(c) *Remaining points of contention*

While there are now examples of research on behavioural diversity that have spanned the subfields of human behavioural ecology, evolutionary psychology and cultural evolution, there are also areas where integration has been less complete. As discussed already, all of the subfields, except gene–culture coevolution, have yet to accept fully the role that genes might play in behavioural diversity. We end by reflecting on other potential points of contention.

(i) *Variation and universals*

We have discussed the argument that the evolutionary psychologists' and human behavioural ecologists' accounts of behavioural diversity can be viewed as compatible by reference to condition-dependent, context-specific strategies. However, from a counter-perspective, subscribed to by some but not all of the authors of this article, there is a limit to how much diversity can be accommodated by this formulation. The potential problem is that the more flexible and variable the exhibited behaviour patterns, the less explanatory power can be attributed to evolved structure within the brain, as the set of required strategies would become unworkably large [67,92]. From this counter-perspective, the more flexible that human behaviour is observed to be, the less *a priori* predictive power evolutionary psychology has. At the extreme, if virtually any behaviour were possible there would be no utility in positing evolved structure, since no insights into underlying mechanism would be provided. Under such circumstances, evolutionary psychology would be reduced to post hoc descriptions rather than predictive hypothesis testing.

As the extent of behavioural diversity becomes appreciated, and in the face of evidence that even apparently basic cognitive processes vary greatly between cultures [93–95], the challenge becomes how to delineate the boundaries of evolved psychological mechanisms in human beings. While evolutionary psychologists have assumed the existence of universal evolved psychological mechanisms, these researchers have only rarely sought evidence for universality. In part, this is because evolutionary psychologists view

universality as axiomatic: evolutionary psychologists start with the assumption that a trait is universal and set out to determine the bounds of variation that it exhibits. However, this stance leads to the concern, at least for some of the authors of this article, that there may be no pattern of variation in an evolved psychological mechanism that would refute the hypothesis that it exists. For instance, what pattern of variation would disprove the hypothesis that humans possess an evolved cheater-detection mechanism? If universality is to be a meaningful concept, minimally evolutionary psychologists will have to make testable predictions concerning the shape, breadth and degree of overlap of the distributions of variation that characterize the behavioural expression of evolved psychological mechanisms. The adjacent discipline of cross-cultural psychology is wrestling with related problems, and has proposed some solutions (e.g. [95]), but has yet to greatly impact the field of human evolutionary behavioural sciences (for exceptions see [93,96–98]).

Finally, if, as one might expect, a universal psychological mechanism would leave a universal imprint in the brain, then a deeper understanding of neural mechanisms, from genes to behaviour and cognition, might eventually shed light on universal cognitive traits. Examining the concept of *immateness* in the light of what is known about the brain function and development will play an important part in this process [99,100]. That, however, would require evolutionary psychologists to expand their remit to investigate underlying brain processes. For the moment, elucidating the details of our evolved psychological mechanisms remains a formidable challenge for the future.

(ii) *Content versus context biases*

We have also emphasized the qualitative difference in the nature of the evolved psychological mechanisms envisaged by evolutionary psychologists and cultural evolutionists. While the former speak of domain-specific, or *content-biased*, evolved psychological mechanisms [17], the latter speak of *context biases*, for instance, mechanisms for copying prestigious individuals or conforming to the majority behaviour [20,101–103]. Moreover, these context biases [101] (also known as *social learning strategies*; [104]) can apply across multiple domains. That is, one can conform with respect to what food one eats and whom one finds attractive (e.g. [105,106]). From the cultural evolutionists' perspective, the evolved structure in the mind is thought largely to specify domain-general learning rules, rather than the domain-specific rules traditionally envisaged by evolutionary psychologists. While advocates of massive modularity might perhaps envisage a conformity rule to be domain specific in a different sense—the domain being something like 'those social inputs on which humans might conform'—even this interpretation must acknowledge that the application of such a rule would cross-cut the more traditionally conceived domains of evolutionary psychology. Moreover, cultural evolutionists recognize a variety of processes that do not necessarily lead to adaptive outcomes [20,46,47], and

accordingly do not expect context and content biases necessarily to converge on the same solutions.

Accordingly, there is more to the difference between cultural evolutionists and evolutionary psychologists than a different emphasis on the relative importance of genes and socially transmitted information: these schools have very different notions of the nature of evolved structure in the mind, and the way in which it facilitates acquired knowledge acquisition. More recently, some evolutionary psychologists have argued the evolved structure of the mind is likely to contain both domain-general and domain-specific mechanisms (e.g. [107,108]; see [109], for an example of a debate between domain-specific versus domain-general explanations of language learning). While we see no reason to expect context biases to *always* be domain general, the observation that they might sometimes be so characterized need not mean any fundamental incompatibility with evolutionary psychology. The degree to which the mind is built of domain-specific versus domain-general mechanisms is an issue that is potentially accessible to empirical investigation, and equally researchers could usefully explore through experimentation whether human behaviour is dominated by content or context biases.

When we begin to consider how content versus context biases impact human behavioural diversity, these discussions inevitably raise the question of whether the distinction between evoked and epidemiological culture is meaningful, as both types of behaviour could be transmitted via social learning processes [110]. The field of cultural evolution has maintained this distinction by paying relatively little attention to the role of genetic variation, evolved content biases or environmental variation in shaping cultural evolution, which are often neglected in their models (see, for instance, [102,103]). While we see considerable value in simple models, ultimately, more general models will be required that take account of these influences. Down the line, model fitting to human behavioural data that change over time and in space may allow the relative importance of these influences to be assessed.

(iii) *Cultural change as an evolutionary process*

It may be more challenging to resolve the controversy surrounding the cultural evolutionists' claim that cultural change is itself an evolutionary process, an argument that has been criticized both by other evolutionists (e.g. [111]) and non-evolutionary anthropologists [112]. This is because there seemingly exist few consensual criteria by which a process may be deemed to be evolutionary. Here, almost all parties would accept that there are some respects in which cultural variants undergo changes in frequency via evolutionary processes, although the exact dynamics of the processes of cultural and biological evolution might differ [113,114], and it is largely a matter of personal preference whether one chooses to emphasize the similarities or the differences. Resolution of this issue, then, will come down to the perceived utility of the cultural evolutionist stance: ultimately, sufficient evolutionists will have to find it useful to regard culture in this manner for the notion to become a central

plank of the human evolutionary behavioural sciences. However, it is hard to envisage how it will be possible to account for the extraordinary behavioural diversity resulting from cumulative culture without some notion of cultural evolution [115].

At present, the fields of evolutionary psychology and human behavioural ecology accept cultural transmission of socially learned information as a source of diversity in human behaviour (e.g. [41]). However, these fields do not typically recognize differential social learning resulting in cultural change as an evolutionary process in itself. Gene–culture coevolution research implies that the history of selection on our species is characterized by a dynamic interaction between genetic and cultural inheritance. From the gene–culture coevolutionist's perspective, human beings have continued to experience substantive evolution right to the present day, with the majority of selective sweeps probably triggered by human cultural activities, and this biological change is likely to have affected cognition [51,116]. At this point, it is unclear how many human genes have been subject to recent selection, what their phenotype and selection pressures were, and how they impact on human behaviour. Once again, this is an issue accessible to empirical investigation, but one that will only be resolved through a multidisciplinary effort involving researchers outside the field of evolution and human behaviour. Whether human behavioural ecologists and evolutionary psychologists are willing to accommodate the idea that some portion of human behavioural diversity could result from genetic differences that have arisen via selection pressures imposed by socially transmitted behaviour remains to be seen.

(iv) *Niche construction*

Early attempts at applying evolutionary theory to human behaviour were heavily criticized for failing to take development into account [70,117]. However, it remains a moot point as to whether the human evolutionary behavioural sciences have adequately addressed the arguments of those developmental and evolutionary biologists that emphasize developmental plasticity and the complex, constructive interplay between the developing organism and the environment [118–120]. In all the approaches discussed so far (with the exception of gene–culture coevolution), the environment is viewed as a pre-existing, external set of cues that can elicit alternative behavioural strategies or that act to trigger a phenotypic response. In contrast, advocates of developmental systems theory, epigenetic inheritance and niche-construction theory have placed emphasis on organisms as active constructors of their environments [118–121]. For these researchers, human beings are seen as bequeathing various legacies to descendent populations: not just genes and culture, but also epigenetic inheritance and constructed components of environments (referred to as 'ecological inheritance'), all of which are potentially sources of behavioural diversity.

From this perspective, human beings are recognized to construct their physical and social environments (for example, by building houses, roads, parliaments

and social institutions), thereby co-directing their own development and evolution [118,122]. Rather than merely being a product of prior selection, niche construction activities are viewed by these researchers as also altering the selective environment in such a way that novel selection pressures can trigger evolutionary episodes, and in a manner that is not adequately accounted for by mainstream evolutionary theory ([118]; see [123], for a counter-perspective). The significance of this perspective here is that it recognizes additional forms of feedback in the evolutionary dynamic, such that human populations are themselves part cause of the environmental variation to which they respond (in figure 1*f*, these interactions are represented by the two-way arrows between G and P). Human behavioural evolution is perceived to involve genetic inheritance, ecological inheritance, natural selection pressures and, importantly, niche construction activities that alter subsequent selection events. One ramification of this is that human populations will create their own behavioural diversity (although this capability is far from restricted to humans).

At present, the fields of evolutionary psychology and human behavioural ecology typically place little emphasis on cultural change as a driver of biological evolution. To the extent that cultural events are acknowledged to be a source of selective feedback on the human genome, they are treated in the same way as a geological event, as a background condition. Here then, is another point of contention. For the gene–culture coevolutionist, treating culture in this way would be equivalent to studying sexual selection by treating female preferences as a background condition—such a stance would, for instance, fail to detect or predict runaway sexual selection, since it would not allow the source of selection to coevolve with the selected trait. This example highlights how modern evolutionary theory sometimes incorporates interactions and feedback between individuals, while at the same time failing to incorporate all interactions and feedback loops between socially transmitted behaviour and the selective environment. For the cultural evolutionist, this kind of gene–culture interactive feedback is likely to be the source of considerable human behavioural diversity, in the same way that sexual selection is recognized to be the source of considerable phenotypic diversity. In this respect, cultural evolutionists and evolutionary psychologists/human behavioural ecologists possess very different explanatory frameworks for understanding behavioural diversity.

5. CONCLUSIONS

The human evolutionary behavioural sciences have historically comprised a number of distinctive sub-fields, each of which provides a different explanation for human behavioural diversity. While these accounts are not necessarily incompatible, and while progress has been made in integrating these perspectives in recent years, there nonetheless remain differences of emphasis and non-trivial points of contention regarding why human beings differ from each other. For instance, researchers disagree on the extent and the nature of evolved psychological mechanisms, differ in their willingness to accept a role of genetic variation

in behavioural diversity, and diverge in their acceptance of socially transmitted information as a key component of the evolutionary process. The articles in this theme issue reflect the span of opinion, and collectively provide a summary of the state of the field. We believe that it is vital that researchers from these different backgrounds work together if we are to build a satisfactory pluralistic, integrative evolutionary account of human behavioural diversity, and we hope that this article and the theme issue in general will act to encourage this collaborative enterprise.

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