What is cultural evolution anyway?

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ABSTRACT

The term cultural evolution has become popular in the evolutionary human sciences, but it is often unclear what is meant by it. This is generating confusion and misconceptions that are hindering progress in the field. These include the claim that behavioural ecology disregards culture. We argue that these misunderstandings are caused by the unhelpful use of term cultural evolution to identify both a phenomenon – culture changing through time – and a theory to explain it – the potential role of cultural transmission biases in driving this change. We illustrate this point by considering recently published influential studies and opinion pieces. If we are to avoid confusion, the term cultural evolution is best reserved to identify the phenomenon of culture, but instead have studied its evolution from the very beginning. Different approaches to the study of human behaviour can coexist and complement each other in the framework offered by Tinbergen's four evolutionary questions. Clarifying key terms is crucial to achieve this synthesis.

Cultural evolution is becoming a blanket term for any kind of human behavioural evolution. However, we believe that this is leading to confusion because the term "cultural evolution" is being used to indicate both a phenomenon – culture changing through time – and an approach to study it – the focus on cultural inheritance and the potential role of transmission biases in shaping culture. This confusing use of the term is widespread in the literature and in informal discussion (we may even have been guilty of this ourselves). For example, Schulz et al. (2019: 1) state that "cultural evolution often favoured some form of cousin marriage". Are they referring to cultural evolution as opposed to genetic evolution? Cousin marriage is surely a culturally transmitted behaviour, so this comparison appears irrelevant here. Or, by cultural evolution, do they mean the action of transmission biases? Or are they referring to the whole phenomenon of cultural change? If so, how can culture changing *per se* "favour" a particular outcome? Innovation, migration, or cultural drift may lead to this outcome, but only some form of selection, genetic or cultural or perhaps both, may "favour" a given outcome.

A second example reveals how this ambiguity can lead to confusion that is hindering progress in the field. A study by Barsbai et al. (2021) shows that human behaviours tightly fit local environmental conditions, following very similar patterns to those shown by mammals and birds living in the same area. In a commentary to the study (Hill and Boyd 2021), the wording appears to present cultural evolution and adaptation to local ecology as alternative explanations for the diversity and distribution of these traits. They state: "Hence, the study appears to validate the basic premise of the evolutionary perspective called 'human behavioural ecology'. However, it is a mistake to conclude from this that culture is unimportant" (Hill and Boyd 2021: 236). This

3

seems to suggest that human behavioural ecology ignores culture. Yet, Barsbai et al. (2021) do not deny that the foraging, reproductive, and social behaviours they examine are culturally transmitted, at least in humans. Neither do they assume that cultural history plays little to no role in shaping the observed patterns, as seems to be implied by Hill and Boyd (2021: 236) when they state: "ecological factors explain much variation in human behaviour, but so too does cultural history". Cultural phylogeny may indeed play a role and, for this reason, the authors control for it in their analyses (Barsbai et al. 2021).

Barsbai et al. (2021) simply show that a variety of human behaviours – almost certainly culturally transmitted – fit local ecology in the same way as behaviours that are probably mostly genetically controlled in birds and mammals. Therefore, their analysis suggests that these cultural traits have been shaped by inclusive fitness interests. In line with a behavioural ecological approach, they are agnostic as to the mechanism leading to this fit. It is possible that it came about through one or more specific biases in cultural transmission or, more generally, because humans are flexible learners that make conscious, strategic choices about what to adopt, sensitive to pay-offs (Burton-Chellew and West 2021). Whilst it is tempting to contrast adaptation to local ecology and "culture" or "cultural evolution" as two competing forces shaping the change of behaviour through time, such a contrast is impossible. As Boyd has acknowledged elsewhere (Boyd 2018), adaptation to local ecology is an outcome of the process of cultural evolution, whereby cultural selection has favoured a set of cultural variants because they are adaptive in a specific environment. Therefore, the tools of behavioural ecology are always going to be needed to understand cultural evolution.

Evolutionary biologists, too, have sometimes used language suggesting this unhelpful dichotomy between adaptation and culture. For example, Burton-Chellew and West (2015: 1043) ask: "Will culture be more important for certain classes of traits such as those less linked to fitness?". We suspect that these authors were meaning to suggest that fitness-insensitive cultural transmission mechanisms can sometimes result in non-adaptive outcomes (especially when a trait is less fitness relevant). However, the way they presented their argument can be potentially misleading. A behaviour can be culturally transmitted, and many human behaviours are, and yet they can still be shaped, at least to some extent, by the inclusive fitness interests of their bearer.

CLARIFYING THE CONFUSION

As testified by the examples above, using the same term to identify both a phenomenon and a theory to explain it is unhelpful. It becomes unclear whether one is referring to an *explanandum* – what we are trying to explain – or an *explanans* – the set of statements we use to explain it (Hempel and Oppenheim 1948). This hinders discussion between researchers employing different approaches, as one may write about cultural evolution as *explanans* and the other might read it as *explanandum*. And it leads to the false dichotomy between culture and adaptation to ecology that we have discussed above.

For these reasons, we believe that the term cultural evolution is best reserved for the phenomenon, not implying any one approach or theory. Just as the phenomenon of organic evolution and Darwin's theory about it are distinct (Brady 1985), so are cultural evolution and our explanations for it. Another term should be used to refer to

approaches centred on cultural transmission (e.g., "cultural transmission approaches" or "social learning approaches").

In this way, it also becomes clear that behavioural ecology does not disregard culture. Behavioural ecologists aim to explain whether and how behaviours serve an adaptive function (Nettle et al. 2013), and most human behaviours are at least partially influenced by transmitted culture. Thus, much of human behavioural ecology studies the cultural evolution of human behaviours. It does so either by exploring the ecological incentives that shape the adoption of specific cultural traits, or by considering culture as part of the environment that determines cost-benefit scenarios faced by individuals (Mace 2014).

Cultural behaviours can be studied from a range of different perspectives. In the 1980s, three evolutionary approaches to human behaviour emerged: evolutionary psychology (which focuses on cognitive adaptations that underly behaviour; Tooby and Cosmides 1990), human behavioural ecology (Nettle et al. 2013), and a third one focusing on cultural transmission (often confusingly referred to as "cultural evolution"). Tinbergen's (1963) four questions about behavioural evolution – mechanism, ontogeny, function, phylogeny – still offer a useful framework for organising this research. They are valid regardless of whether a behaviour is genetically controlled, culturally inherited or a bit of both – and they are complementary. Rather than being mutually exclusive, these three evolutionary approaches simply tackle human behaviour, including cultural traits, at different levels of explanation (Figure 1). Suggesting a dichotomy between culture and adaptation to local ecology, though perhaps intuitively appealing, is misleading: it generates confusion between function and ontogeny.

6

BOTTOM-UP OR TOP-DOWN?

Models of cultural transmission derived from population genetics seek to predict the distribution of cultural phenotypes bottom-up, from transmission processes such as conformity bias. This does not mean that these models and related hypotheses disregard adaptation. In fact, major theorists have proposed that transmission biases have been selected for because they facilitate the spread of adaptive solutions via social learning (Boyd and Richerson 1985; Boyd 2018). However, the emphasis on transmission dynamics means that when addressing cultural phenotypes, mechanistic explanations are favoured. In contrast, behavioural ecologists seek to predict the distribution of cultural traits top-down, from the adaptive problems they are designed to solve. In many cases, the top-down approach might generate results more readily than the bottom-up approach. With social learning processes showing few general rules (as multiple mechanisms are likely to be acting at the same time), predicting cultural diversity from the mechanisms of social transmission is going to be very hard.

Models informed by inclusive fitness, and their test in the field, are key to help us understand cultural diversity; they build a clearer picture of the diversity of human behaviour than cultural learning approaches alone can do. Cultural transmission dynamics can sometimes prevent the realisation of inclusive fitness interests; more empirical research is needed to establish when this is indeed the case (the demographic transition from high to low fertility is one candidate; Colleran 2016). Yet, contrary to some suggestions, this does not mean that fitness-based models are inadequate or that only transmission dynamics should be prioritized as a matter of course.

7

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FIGURE LEGENDS

Figure 1

Human behavioural ecology, evolutionary psychology and the cultural transmission approaches (shown in green, blue and brown, respectively) ask different evolutionary questions about human behaviours. Notice that some might extend the domain of interest of the cultural transmission approaches to include mechanism, and others might extend evolutionary psychology to cover ontogeny, depending on what definition of psychological mechanism is adopted.