Cultural selection and biased transformation: two dynamics of cultural evolution

Alex Mesoudi *

27 November, 2020

*Human Behaviour and Cultural Evolution Group, Biosciences, University of Exeter, Penryn, Cornwall TR10 9FE, United Kingdom; a.mesoudi@exeter.ac.uk

Abstract

Here I discuss two broad versions of human cultural evolution which currently exist in the literature and which emphasise different underlying dynamics. One, which originates in population-genetic-style modelling, emphasises how *cultural selection* causes some cultural variants to be favoured and gradually increase in frequency over others. The other, which draws more from cognitive science, holds that cultural change is driven by the *biased transformation* of cultural variants by individuals in non-random and consistent directions. Despite claims that cultural evolution is characterised by one or the other of these dynamics, these are neither mutually exclusive nor a dichotomy. Different domains of human culture are likely to be more or less characterised by cultural selection and biased transformation. Identifying cultural dynamics in real-world cultural data is challenging given that they can generate the same population-level patterns, such as directional change or cross-cultural stability, and the same cognitive and emotional mechanisms may underlie both cultural selection and biased transformation. Nevertheless, fine-grained historical analysis and lab experiments, combined with formal models to generate quantitative predictions, offer the best way of distinguishing them.

Keywords: biased transformation; cultural evolution; cultural selection; social learning.

Main text word count (including figure captions, excluding abstract and references): 7729

Number of figures: 4

Number of tables: 0

1 Introduction

Does culture 'evolve'? Can socially transmitted behavioural traits such as languages, attitudes, technological inventions, religious beliefs, scientific theories and so on, be understood as changing over time in a way comparable to how biological species change over time? Such a comparison was drawn by historical linguists long before Darwin wrote *The Origin of Species* [see 1], and was made by Darwin himself in *The Descent of Man* [2]. However, it was not until the 1970s and 1980s that serious attempts to formalise the idea of cultural evolution appeared [3–5]. These seminal works borrowed the tools of mathematical population genetics and adapted them to culture, creating models that assume behavioural traits *vary* across individuals, are *inherited* socially (not genetically) via imitation, language, teaching or other means of social learning, and can be subject to *selection* wherein some traits are more or less likely to be passed on than others, as well as non-selective dynamics in the form of cultural drift.

These models explicitly recognised differences between genetic and cultural evolution, such as the possibility of acquiring cultural traits from a wide range of individuals, not just the two parents from whom we acquire our DNA [5], and various biases by which we do this, such as conforming to the majority trait in one's group [3]. In the last two decades there has been an exponential increase in cultural evolution research inspired by this groundwork [6], with evolutionary concepts, tools and methods used to explain cultural variation and change in domains such as language, technology, religion, political systems, family dynamics, migration and acculturation, music, art, literature and more [7–10]. The notion that cultural change represents an evolutionary process is more than a philosophical curiosity; it potentially provides powerful new theoretical and methodological tools for understanding cultural change and variation that can significantly enhance and perhaps even synthesise the social and behavioural sciences [11–13]

Yet there remains an underlying and ongoing tension concerning the extent to which cultural change resembles the process of genetic evolution[1]. Two broad approaches can be recognised.

[1]In the following I have intentionally avoided identifying traditions with particular scholars or sets of scholars, or with particular geographical regions. Such identification often triggers social identity-related groupishness and defensiveness. I have tried instead to focus on the distinctive theoretical and intellectual aspects of each broad

First, scholars more closely rooted in the tradition that began with the aforementioned population-genetic-style models tend to focus on how selection-like learning biases cause some cultural variants to be favoured and gradually increase in frequency over others [9,14–17]. Such learning biases include preferentially copying older, prestigious or successful individuals (sometimes called 'context biases'), or preferentially copying certain kinds of traits over others (sometimes called 'content biases'), such as stories that are emotionally salient or tools that are particularly effective [16,18,19]. 'Copying' here is assumed to be relatively faithful, reflecting claims that humans possess unique psychological adaptations for high fidelity social learning [20,21]. Less explanatory weight is placed on how individuals create, modify and transform cultural traits as sources of directional cultural change (although this is acknowledged to occur; see below). Cultural change is seen instead as primarily a population-level process, where small, often random changes (akin to cultural mutation [5]) that happen to be effective are selectively copied over time. This leads to an emphasis on cultural evolution as a cumulative, population-level process that often exceeds any one individual's understanding or ability [22,23], and accounts for our species' distinct ecological success [14]. Examples of work in this tradition include field studies showing that pregnancy-related food taboos are preferentially learned from mothers and prestigious older women [24], lab experiments showing that more complex tools are maintained in larger groups due to the availability of more demonstrators from whom to learn [25], and historical analysis of Go matches showing that opening moves spread by being copied from successful players [26].

Other scholars see cultural evolution differently [27–32]. Inspired more by cognitive science than population genetics, here cultural change is seen as primarily resulting from the directional transformation by individuals of culturally acquired information. According to this view, the acquisition of cultural information is rarely a case of high fidelity copying. Rather, it is a process of transformation and reinterpretation that may be affected by the receiver's cognitive biases, pre-existing knowledge, individual learning, or the dynamics of communication and interaction between sender and receiver. Consequently, directional cultural change is seen as resulting from the directional transformation of information by individuals. Where individuals transform representations in the same direction, such as due to a universal feature of human cognition or a similar ecological or envi-

position. Naturally, there are also many exceptions and overlap across the broad positions.

ronmental pressure, then representations will converge on a stable type or form, sometimes called a 'cultural attractor' [29–31]. Consequently, there is more focus on explaining cross-cultural regularities (rather than diversification and cumulative change) that reflect individual-level psychological processes (rather than exceeding individual-level understanding). This approach has also been explored in the context of Bayesian models of cultural evolution, where individuals possess inductive biases - constraints on learning and memory - that shape their priors when evaluating information received from other individuals [32,33]. Over successive transmission episodes, representations gradually transform according to, and converge on, individuals' inductive biases. Finally, this dynamic also has precedence in the earlier population-genetic inspired approach discussed above. Early models of 'guided variation' [3] involved individuals non-randomly improving cultural traits via reinforcement or other forms of individual learning, with such traits then culturally transmitted in an unbiased, non-selective manner. Again, these models show that guided variation causes cultural evolution to converge on the cultural traits that are favoured by individual learning.

Examples of this second approach to cultural evolution include the cross-cultural convergence on blood-letting as a medical practice [34], on direct eye gaze in portraits rather than averted gaze [35], and on common colour terminologies [36], all of which are argued to reflect psychologically 'attractive' forms. Lab experiments simulating Bayesian inductive biases have shown how participants independently converge on common priors, such as linear relations between variables [32], compositionally structured languages [37] or visually symmetrical arrowhead dimensions [38].

These two versions of cultural evolution emphasise different dynamics, which I will call *cultural selection* and *biased transformation* respectively[2]. In evolutionary terms, cultural selection assumes small and often undirected cultural mutation followed by the selection of beneficial variants via non-random learning biases, with the latter selection-like process primarily driving cultural change. Biased transformation comprises substantial and directional mutation at the individual level which

[2] Some of the scholars who I cite in association with cultural selection, e.g. [3], avoid the term 'selection', preferring 'transmission bias'. Others do use the term, e.g. [5]. It seems to me that the process of selectively copying certain other individuals (e.g. those high in prestige) or certain types of traits (e.g. more effective tools) justifies use of the term 'selection', and is appropriate given the foundation of this tradition in population-genetic models. Many of the scholars who I cite in association with biased transformation often use the term 'cultural attraction', but I will avoid this term due to its ambiguity [39,40], and due to the fact that sometimes selection-like learning biases such as conformity are included within it [29]. The term 'biased transformation' is used frequently in [30] to describe the core mechanism of the cultural attraction approach, and so seems a suitable description of its key assumption.

is primarily responsible for driving cultural change, rather than population-level selection-like learning biases.

It has been pointed out by some scholars [41–44] that these two dynamics represent the two terms in the Price Equation [45,46], a commonly-used abstract formalisation of the evolutionary process. The first term of the Price Equation represents change due to (cultural) selection of traits due to their fitness effects, and the second represents change due to (biased) transformation of traits from one generation to the next. While the latter transformation term is often assumed to be negligible in genetic evolution, the same is not the case for cultural evolution, such that biased transformation may be a directional source of cultural change[3].

2 Disagreements over the dynamics of cultural evolution

Several researchers have drawn the conclusion that, if biased transformation plays a causal role in cultural change - in terms of the Price Equation, if the second biased transformation term is non-zero - then cultural change should not be described as 'Darwinian', and/or that methods borrowed from biology (e.g. population genetic modelling) are inappropriate [29,44,47,48]. For example, "it would seem reasonable to reserve the category 'Darwinian' for cases where . . . there is a prominent role for selection rather than transmission in explaining design-like properties" [44], p.7. Or, "in order to model cultural evolution, we must not simply adjust existing replicative or selectional models to fit the cultural case" [29], p.2. Furthermore, rather than focusing on population-level dynamics and selection-like learning biases, which are characteristic of cultural selection, it is argued that a more

[3]This is not, however, as clear-cut as often portrayed (F.J. Weissing, pers comm). Strictly, the second term in the Price Equation can only be equated solely with trait transformation/transmission if selection is very weak and frequency-independent. Otherwise, the second term will be affected by factors other than transformation, such as changes in the environment, and even in genetic systems will often be non-negligible (otherwise, fitness would always increase or stay constant, given that the first term in the Price equation, when applied to fitness change, is a variance and hence non-negative; on the contrary, in genetic evolution fitness may decrease, implying that the second term must be negative). Given that cultural selection is unlikely to be very weak, and is often frequency-dependent (e.g. in the case of conformity), these conditions are unlikely to hold for cultural evolution. This means that the second term cannot be straightforwardly equated with 'transformation'. There are also several other caveats and complications with applying the Price Equation to cultural evolution [41,44]. For these reasons, I do not focus my analysis primarily on the Price Equation, and in the models I implement cultural selection and biased transformation in a more concrete manner.

appropriate approach would be to focus on individual cognition, which, if biased transformation is the predominant driver of cultural change, may be sufficient to explain the direction of cultural change. For example, "[n]ovel concepts and mechanisms, more inspired by cognitive sciences and less by population genetics, are required [to explain cultural evolution]" [48], p.21 or "advances in understanding the population distribution of cultural practices or representations seem most likely to come from cognitive science... No isomorphism to Darwinian evolution is required in order to do this" [44], p.8.

On the other hand, researchers who emphasise cultural selection have tended to downplay the importance of biased transformation for explaining cultural change. For example, one model concluded that even (actually, especially) when biased transformation is strong, the long-term cultural dynamics and the final equilibrium of a cultural trait are both determined by cultural selection [42]. According to this model, biased transformation reduces to cultural selection. Furthermore, while biased transformation is acknowledged in seminal texts (e.g. 'guided variation' in [3], as noted above), in practice much more attention has been given to cultural selection learning biases such as those related to prestige, conformity and content biases [16,18,19].

3 Two models of cultural selection and biased transformation

Words are imprecise means of communicating ideas. Formal models can help make this imprecision more precise, and reveal the often hidden assumptions of purely verbal models [49]. Consequently, here are two very simple individual-based models of cultural selection and biased transformation to illustrate what I mean above, and to draw some very simple insights. Model 1 simulates cultural selection and biased transformation within a single population to examine how each dynamic generates cultural change. Model 2 extends this to multiple populations and cumulative culture, to examine claims of cross-cultural stability and diversification. The R code for both models is available at https://github.com/amesoudi/culturalselection_biasedtransformation, and readers can play with them without needing to run the code at https://amesoudi.shinyapps.io/CSBT_model1/ and https://amesoudi.shinyapps.io/CSBT_model2/.

These models are intended to complement previous models that examine these cultural dynamics [3,38,42,47,50–52]. The insights are not particularly novel compared to these previous studies, but (i) they provide a replication and confirmation of previous models' results using different assumptions and implementations, thus contributing to a broad family of models addressing the same issue (which is often better than seeking a single 'perfect' model: [49]); (ii) their insights are integrated below with more recent empirical studies and placed within the context of ongoing debates concerning the nature of cultural evolution; and (iii) full code and interactive online versions of the models are provided alongside this paper, to allow others to directly explore the results and extend the models using different assumptions.

3.1 Model 1: Within-population dynamics

In Model 1, each of n individuals possesses a value of a continuously varying culturally transmitted trait which ranges from 0-100. In this model, cultural selection and biased transformation are assumed to act in the same direction, towards 100. Hence, higher values of the trait indicate both higher-payoff traits that are favoured by cultural selection, and/or more individually attractive traits favoured by biased transformation. The n individuals are initialised with trait values drawn from a normal distribution with mean of 10 and standard deviation of 1, giving slightly different values centred around a relatively low value.

In each time-step, all n individuals are replaced with n new individuals. This can be seen as a new biological generation, or a new instantiation of the same population at a new time following cultural transmission. These n new individuals first each choose a demonstrator from the previous time-step from whom to learn (Fig 1). Cultural selection is implemented via payoff-biased social learning. With probability s, each individual selectively adopts the highest-value trait from the individuals of the previous time-step. With probability $1 - s$, they adopt the trait value of a randomly-chosen individual from the previous time-step. Random copying is, by definition, non-selective.

Biased transformation, as well as unbiased transformation / cultural mutation, is then implemented via the modification of the chosen demonstrator's trait value (Fig 1). The chosen demonstrator's trait value is modified by an amount drawn from an exponentially modified Gaussian (EMG) distribution [53]. This distribution combines a normal/Gaussian distribution (with mean μ and standard deviation σ) with an exponential distribution (with scale parameter β) to give a distribution that is directionally skewed when $\beta > 0$. Specifically, the mean of the normal distribution μ is set to zero, i.e. no change to the trait value of the chosen demonstrator. Random deviation to this copied value is introduced when the standard deviation of the normal distribution σ is greater than one. This can be seen as random copying error, or blind, undirected attempts at modifying the trait following transmission, akin to cultural mutation [5]. The skew introduced by the scale parameter β generates biased transformation. When $\beta > 0$, the skewed distribution makes individuals more likely to transform the trait in the direction of the biased transformation, i.e. towards 100. Note that there is no gene-like replication in this model (unless $\sigma = 0$ and $\beta = 0$ such that the adopted value is exactly the same as the demonstrator's, but in this case there is also no evolution), and biased transformation is probabilistic not deterministic: biased transformation can sometimes lead to values in the opposite direction to the bias, even when β is large.

3.2 Discussion of Model 1

The results of Model 1 are shown in Fig 2. The first column shows, as both intuition and previous models [3,44] predict, that both cultural selection and biased transformation drive the cultural trait towards the value favoured by each of them, i.e. the maximum value of 100. This replicates a point made in [44]: directional change in cultural evolution may be caused by either cultural selection or biased transformation (or both, as shown in the bottom row of the first column). Observing that a particular cultural trait has spread, be it a tool, word, song, folk tale or religious belief, therefore does not provide evidence that cultural selection was responsible for that spread [44]. For example, one recent study claimed that certain grammatical forms, such as the regularisation of past tense verbs, spread due to "selection in language evolution" [54]. Yet what they actually showed was that these grammatical forms showed a directional increase in frequency, which is consistent with either cultural selection or biased transformation (or both combined).

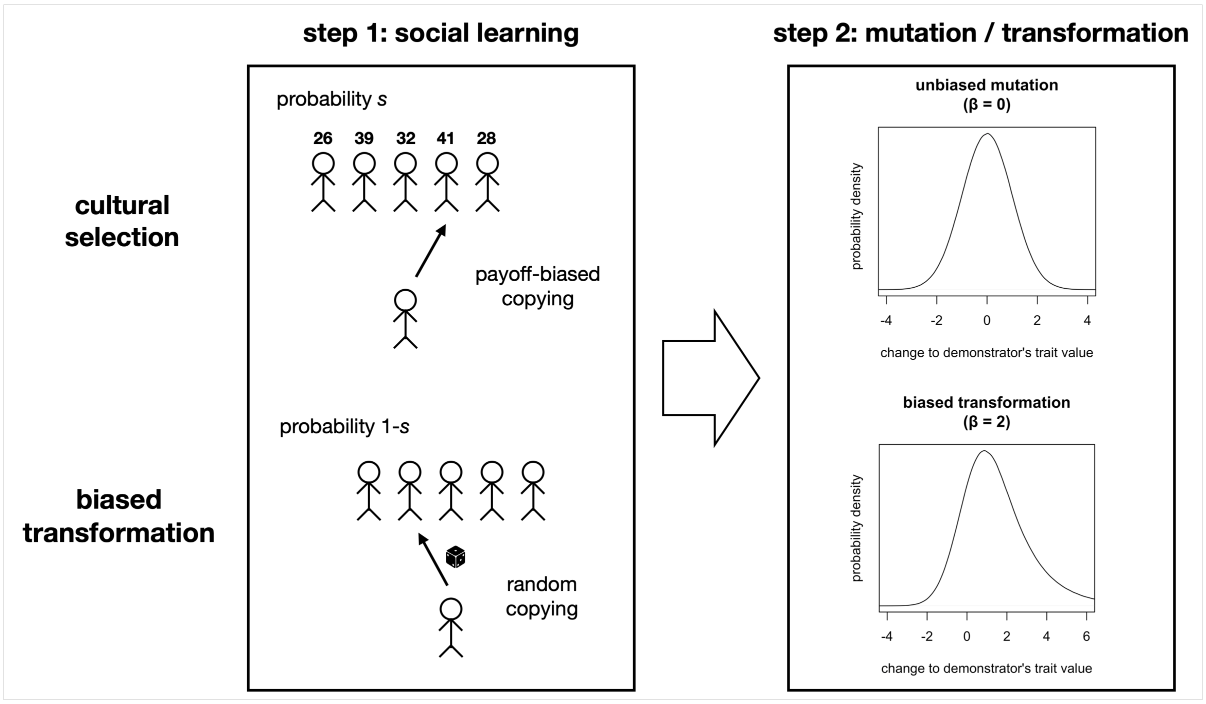

Figure 1: Outline of Model 1. In step 1, individuals choose a demonstrator from whom to socially learn. With probability s they choose the demonstrator with the highest-payoff trait, characteristic of cultural selection, and with probability $1 - s$ they choose a demonstrator at random, which by definition is non-selective. In step 2, they modify the chosen demonstrator's trait by drawing a value from an exponentially modified Gaussian (EMG) distribution, with mean and standard deviation of the normal distribution component set to zero and one respectively, and which is then added to the demonstrator's trait value. When the scale parameter of the exponential component of the EMG, β, is zero, then this modification is entirely random, thus implementing unbiased cultural mutation (akin to genetic mutation). When $\beta > 0$, the values are more likely to be drawn from the upper end of the distribution, thus implementing biased transformation. The upper parts of each box are characteristic of cultural selection, while the lower parts are characteristic of biased transformation, although the continuous parameters s and β allow a mixture of these two dynamics to occur together.

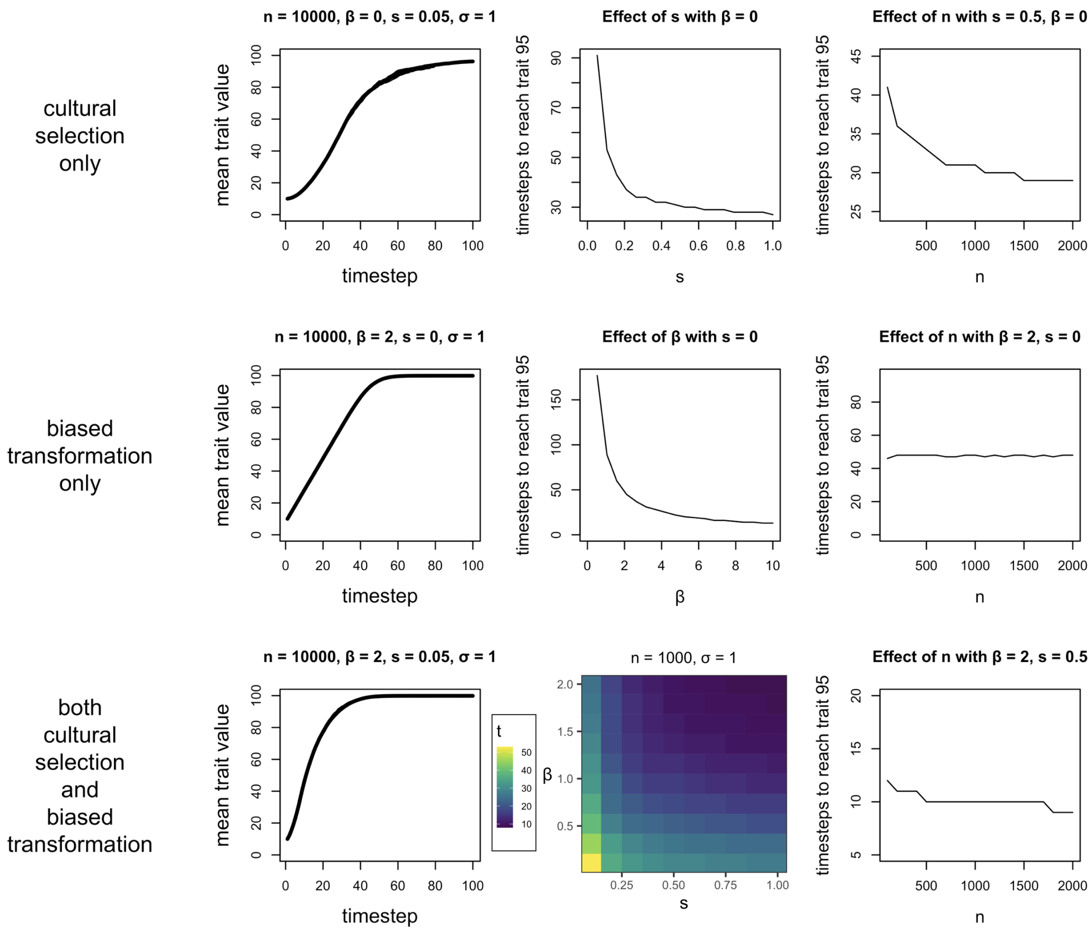

Figure 2: Results of Model 1. The top row shows results representative of cultural selection dynamics, the middle row those of biased transformation, and the bottom row of both dynamics acting simultaneously. The first column shows time series (aka 'diffusion curves'), where either cultural selection (via s) or biased transformation (via β) or both drives the culturally transmitted trait to its maximum value, which is the value favoured by both cultural selection and biased transformation. The second column shows the effect of different values of s or β on the number of timesteps taken to reach its maximum value (specifically, to reach a trait value of 95, given that 100 may not be reached due to mutation). In the first two cases, as cultural selection or biased transformation increase in strength, the faster is the spread of the favoured trait. The middle bottom panel shows a heatmap of the same measure (t = timesteps until trait 95 is reached) for different non-zero combinations of s and β. The final column shows the effect of population size, n, on time to reach the maximum. Here, cultural selection is more effective in larger populations, while population size has no effect on the action of biased transformation. When both dynamics are acting, there is a weaker effect of population size. n = number of individuals, β = strength of biased transformation, s = probability of cultural selection, σ = random, undirected mutation. All results are the average of 10 independent simulation runs.

However, this works the other way too. It does not necessarily follow that all instances of directional change are therefore due to biased transformation. For example, the demonstration that direct eye gaze in portraits has increased in frequency over time [35] does not necessarily mean, as claimed in the original study, that this was due to biased transformation as individual artists modified their style from averted to direct eye gaze. It could equally have been cultural selection, with novice portrait artists preferentially copying other artists that painted direct eye gaze, or preferentially copying direct eye gaze portraits, rather than individually transforming their style from averted gaze to direct gaze. Or it could have been a mixture of the two dynamics, with preferential copying of direct eye gaze artists or portraits, combined with individual transformation towards direct eye gaze.

How then can we distinguish between cultural selection and biased transformation in real-life instances of cultural evolution? Fig 2 provides some suggestions. The first column shows that cultural selection is characterised by an s-shaped diffusion curve, which starts slow, increases in rate, and then levels off. Biased transformation is characterised by an r-shaped diffusion curve, which increases at a constant rate until reaching the maximum. It has been suggested that diffusion curve shape can be used to distinguish cultural selection and biased transformation [55], and because most diffusion curves in the diffusion of innovations literature in sociology are s-shaped [56], that the typical mode of technological and social change in human societies is driven by cultural selection rather than biased transformation [55]. Non-human social learning researchers have also used s-shaped diffusion curves to argue that certain behaviours spread via social rather than asocial learning [57]. Unfortunately, however, the use of diffusion curve shape to infer learning dynamics has been deemed unreliable since it was shown that s-shaped curves can also be generated by non-cultural selection dynamics under certain circumstances, such as when there is individual variation in the strength of biased transformation [58,59].

The final column of Fig 2 shows another difference. As is well known from evolutionary biology, the strength of natural selection depends on the variation in the population (known as Fisher's Fundamental Theorem). In principle, the same applies to cultural selection. Consequently, cultural selection is more effective in larger populations where there is more variation upon which to act.

Biased transformation, on the other hand, is an individual-level process. Transformation occurs at the same rate irrespective of what trait values others in the population possess. Consequently, biased transformation shows no relation to population size (see [50,52] for similar findings).

This links to an ongoing debate concerning the effect of population size and other demographic factors in cultural evolution [25,60–63]. There has been much back and forth between those who argue that the rate of cultural evolution is partly determined by population size [61,62] and those who argue that it is not [63]. While some of this debate concerns the reliability of the empirical record, it may be worthwhile turning the debate on its head. Perhaps those instances where population size *does* seem to determine the rate of cultural evolution, mostly relating to technology [61,64], can be taken as evidence of cultural selection operating in that domain. Instances where population size does *not* seem to affect the rate of cultural evolution, as observed for example for folk tales [65], can be taken as evidence of biased transformation operating in that domain. However, this requires overcoming empirical issues surrounding estimates of population size and structure [60], measures which may not always be available or reliable.

Alternatively, there can be more direct examination of cultural variation and change to explicitly test for cultural selection and biased transformation. This requires going beyond population-level signatures and delving into the history and function of specific cultural traits. For example, one innovative study examined the long-term cultural evolution of the "f-holes" in violins [66], the holes in the body of the instrument that improve sound quality by enhancing acoustic conductance. These holes gradually evolved over several centuries from relatively ineffective circular holes in the 10th century to the now-standard f-holes in the 18th century, which hugely enhance sound quality. Using formal analysis of the variation in hole shape over time, it was shown that this change in shape was so gradual as to be consistent with random, undirected changes introduced by each generation of violin-maker due to imperfections in the manufacturing process. Within each generation, those violins that happened to sound better were selectively copied, and those that happened to sound worse were not. There were no disruptive or directional changes within generations, and no evidence that violin-makers were directionally transforming the hole shapes to improve sound quality. This is probably because the effects of violin holes on acoustic conductance are complex, opaque and unintuitive. It is not cognitively intuitive that f-shaped holes give better acoustic conductance than any other shaped hole, and the design space of possible hole shapes combined with possible violin designs is too vast to easily solve with trial and error within a single lifetime.

There were even counterexamples to demonstrate this point [66]. In two cases (Savart's trapezoidal design and Chanot's guitar-shaped design), early 19th century violin makers attempted to use contemporary scientific principles to create novel violin designs that were beyond the normal range of random variation. Yet these designs had poorer acoustic properties than the standard designs, and are now-forgotten evolutionary dead-ends. This study therefore provides quantitative evidence not only that the dynamics of cultural selection - small, undirected, random variation plus selective copying - were responsible for the cumulative cultural evolution of violin designs, but that this makes adaptive sense given the complexity and opacity of this particular cultural trait.

As well as historical analyses, one might also use lab experiments to obtain independent evidence that an instance of directional change is consistent with biased transformation or cultural selection. For example, one study which argued that blood-letting as a medical practice has independently emerged cross-culturally due to biased transformation presented a series of lab experiments showing that (i) stories containing blood-letting are more memorable, and persist for longer, than equivalent stories involving other therapies, and (ii) descriptions of accidental cuts can spontaneously transform into stories about blood-letting [34]. This provides independent evidence that individual cognition drives biased transformation to favour blood-letting, lending plausibility to the claim that biased transformation has generated the cross-cultural stability of blood-letting in actual human societies.

We should be cautious, however, in drawing too strong conclusions from lab experiments, and too closely identifying biased transformation with cognition. It is possible that the same cognitive mechanism can underpin both biased transformation and cultural selection[4]. For example, experimental

[4]By 'cognitive mechanism' I mean a bias to attend to, process or recall information in a particular way. Such a mechanism would operate at a lower level than broader cultural 'dynamics' such as cultural selection and biased transformation, which describe how cultural traits are transformed and transmitted by and between individuals. Hence, cognitive mechanisms and cultural dynamics are alternative (and complementary) levels of analysis. Generally, it is desirable to unpack higher-level descriptions of social learning strategies (e.g. the 'payoff-biased copying' that I use as a form of cultural selection here) into their underlying psychological mechanisms [67].

studies using the transmission chain method [68], where information is passed from individual to individual along linear chains, have identified an advantage for emotionally salient information in cultural evolution, particularly content that elicits a reaction of disgust [69,70]. However, this could in principle occur via either biased transformation or cultural selection (or both): individuals may directionally transform what they receive from others to make it more disgusting (biased transformation), and/or they may preferentially attend to, acquire and pass on more disgusting material than less disgusting material (cultural selection).

One study demonstrated that both of these dynamics are present and can cause the spread of disgusting information as people both transformed *and* selectively acquired and passed on disgusting material [69]. Most transmission chain experiments, however, can by design only detect transformation [68]. It is sometimes argued that because a particular form is favoured at the end of an experimental transmission chain [71], then this indicates that biased transformation is the dominant force in real-world cultural evolution [32]. Yet without explicitly demonstrating that the same directional change could not also be generated by cultural selection, such a strong conclusion may not be warranted. Similarly, other effects documented experimentally using the transmission chain method, including advantages for social information [72,73], minimally counter-intuitive concepts [74] and negative information [75,76], may be equally effective when operating via cultural selection as they have been demonstrated to be via biased transformation.

Finally, we can also draw a parallel between payoff-biased social learning (the form of cultural selection that is assumed in Model 1; see Fig 1), where traits associated with higher monetary, social or reproductive payoffs are preferentially copied, and the form of biased transformation modelled in [3] as guided variation, in which traits that are associated with higher payoffs are reinforced during an individual's lifetime via instrumental conditioning. In both cases, a psychological preference for high payoffs causes an increase in high-payoff traits, in the former via cultural selection, and in the latter via biased transformation. The general point here is that the same cognitive, social or emotional mechanisms can underlie both biased transformation and cultural selection. We should therefore not necessarily identify biased transformation specifically with 'cognition', when the same psychological mechanisms may also underlie cultural selection dynamics.

3.3 Model 2: Between-population dynamics and cumulative culture

Another common claim is that biased transformation can explain cross-cultural stability, i.e. similarity in cultural traits across different populations, societies or groups. Sometimes this is turned around: that evidence of cross-cultural stability in a particular trait can be taken as evidence for the operation of biased transformation [30]. Yet it seems logical that cultural selection can also generate cross-cultural stability. One way it can do this is if there is a single high-payoff trait on which cultural selection converges, as in Model 1. If there are multiple high-payoff traits, i.e. multiple cultural lineages, then cultural selection may generate cross-cultural divergence if different populations converge on different solutions to a problem. However, if there is some migration or inter-cultural transmission [51], then again multiple populations may converge on the same solution. Model 2 simulates this latter scenario.

Assume now that there are discrete cultural traits structured as shown in Fig 3. There is a single intuitive or attractive trait, X. This might be blood-letting as a medical practice, for example. Assume it has a payoff of zero, and that the same biased transformation process as implemented in Model 1 favours trait X (in fact, blood-letting is suggested to decrease fitness due to the greater chance of blood infections [34], but for our purposes fitness neutrality is a reasonable conservative assumption). There are also three trait lineages, A, B and C, representing increasingly effective (high payoff) solutions to the same problem. They might represent, for example, herbal medicine, allopathic medicine, and surgery. Each lineage has five cumulative levels. These are cumulative in the sense that the preceding trait (e.g. B3) must be known before the subsequent trait (e.g. B4) can be acquired, and they increase in payoffs (e.g. B4 has higher payoff than B3). Consequently, the same cultural selection process as implemented in Model 1, selective payoff-biased social learning, favours increasing levels of each lineage. Unlike Model 1, therefore, in this model biased transformation and cultural selection act in opposite directions: biased transformation towards trait X, and cultural selection away from trait X. Finally, the lineages may vary in their payoffs for equivalent traits. When $d > 0$, then traits in lineage C have higher payoffs than the equivalent traits in lineage B, and traits in lineage B have higher payoffs than the equivalents in lineage A.

To examine cross-cultural stability, we assume g groups each containing n individuals. In each time-step, individuals in each group first select a demonstrator from within their own group. As before, they select the demonstrator with the highest payoff with probability s, and a random member of their group with probability $1 - s$. This is cultural selection. Their final adopted trait is determined by a similar process of biased transformation as in Model 1, but modified to handle discrete traits[5] and always favouring transformation towards X. For example, if the demonstrator has trait A4, when $\beta > 0$, then A3 is more likely to be adopted than A5. As in Model 1, the process is probabilistic, so movement in the opposite direction is also possible; this is how high-payoff traits appear that are then favoured by cultural selection when $s > 0$. Finally, there is migration. With probability m, each individual moves to a new group chosen at random (Wright's island model; see [51] for details). This can be seen as either individuals actually moving to a new group and taking their traits with them, or a process of inter-group transmission as a member of one group interacts with and adopts the trait of a member of another group.

3.4 Discussion of Model 2

Representative results are shown in Fig 4. As expected, when biased transformation is the only process operating (Fig 4, top), then we see cross-cultural stability as each group converges on the intuitive, attractive trait X. While the probabilistic process of biased transformation sometimes leads to the emergence of high payoff traits, in the absence of cultural selection to select these traits, biased transformation drives cultural evolution back to trait X. When cultural selection is the only process operating (Fig 4, middle), then we see cross-cultural divergence. Each group converges on the highest-payoff trait within a different lineage (note that, by chance, sometimes groups can end up independently converging on the same trait; this would be an instance of convergent cultural evolution and is not shown in Fig 4. However, if there are a large enough number of

[5] To modify the biased transformation process to handle discrete traits, a continuous number is drawn from an EMG distribution with a Gaussian mean of zero, standard deviation σ (typically set to 1), and exponential scale parameter β, as in Model 1. If this value lies between -1 and 1, then the individual adopts the demonstrator's trait with no modification. If the value is greater than 1, then the individual adopts the next trait in that lineage closest to X (e.g. C4 becomes C3; A2 becomes A1). A1, B1 and C1 all become X. If the value is less than -1, then the individual adopts the next trait in that lineage in the opposite direction (e.g. C4 becomes C5; A2 becomes A3). Lineages are bounded at X and A5/B5/C5. All individuals start with no trait before initially acquiring trait X.

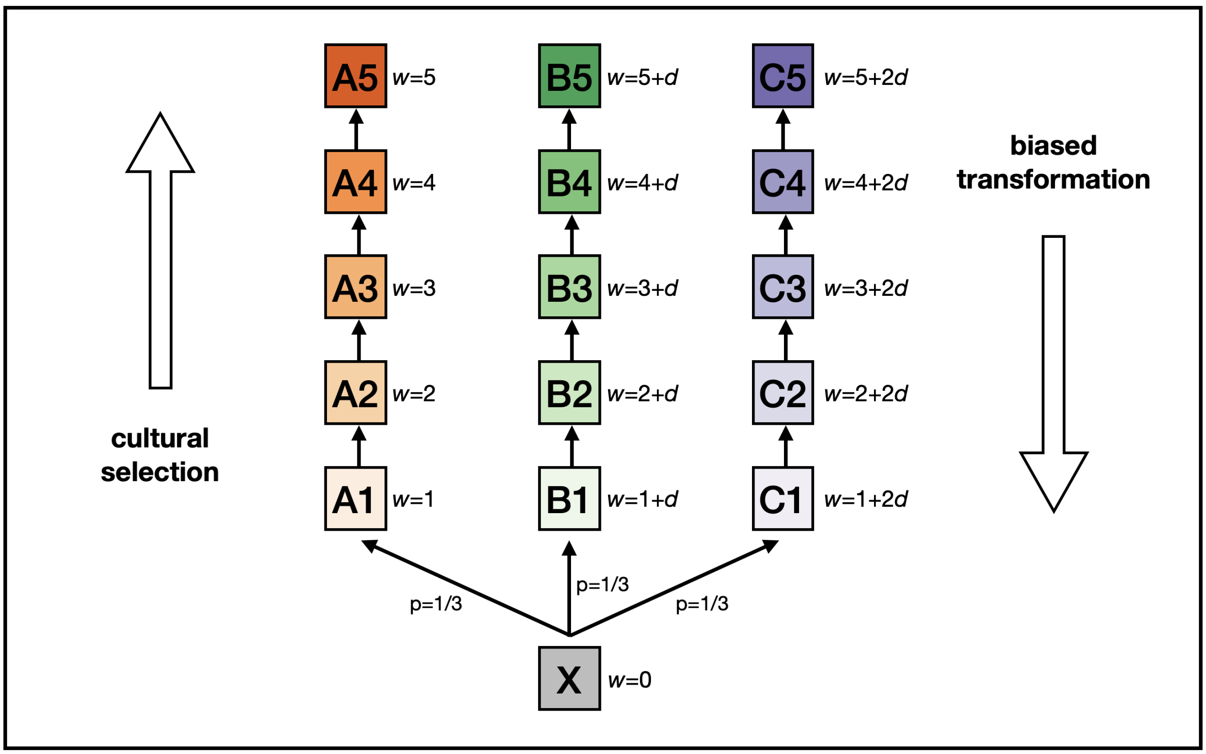

Figure 3: Trait structure in Model 2. There is a single intuitive, cognitively attractive trait, X, which is favoured by biased transformation. Cultural selection, in the form of payoff-biased social learning, favours traits along three trait lineages, A, B and C. These lineages comprise five traits each (A1-A5, B1-B5 and C1-C5), with each level increasing in payoff (w). Cultural selection therefore favours traits higher in each lineage. In addition, when $d > 0$, the equivalent traits in lineage C have higher payoffs than lineage B, and those in lineage B have higher payoffs than lineage A. The initial transition from trait X to either A1, B1 or C1 is equally likely (p=1/3 for each).

groups relative to number of trait lineages, then some divergence would be expected). Finally, when cultural selection is combined with a small amount of migration or inter-group contact (Fig 4, bottom), then each group converges on the highest-payoff trait from the highest-payoff lineage, trait C5. Hence we see cross-cultural stability resulting from cultural selection plus a small amount of migration / inter-group contact. Migration has no effect when biased transformation is the dominant cultural dynamic as in the top panel of Fig 4, because almost every individual in every group already possesses the same trait X[6].

The convergence on high payoff traits due to cultural selection plus migration resembles the advantage of partial connectivity shown in previous lab experiments [77] and models [78]. This occurs when there are multiple traits varying in payoff, and when relatively infrequent migration or intercultural contact causes high payoff traits to spread across groups. Full connectivity can lead to the premature convergence on a low payoff trait, while no connectivity prevents convergence of any kind. For our purposes, it does not matter so much whether convergence is premature and suboptimal, just that cultural selection plus migration (or some kind of inter-group contact) generates cross-cultural stability.

How then can we distinguish between cross-cultural stability due to biased transformation and cross-cultural stability due to cultural selection plus migration? Historical analysis will be useful here given that the former should show no cumulative change, while the latter should. The presence of prior, less effective forms of a trait would indicate cultural selection. One might also track instances of migration or between-society contact that bring traits across historical group boundaries, which would indicate convergence via cultural selection. Again, violin f-holes might be a good real-world example of both of these cases, given that they were shown to gradually improve over several centuries towards higher-payoff (i.e. better acoustic quality) forms, and that all modern violins have converged on the same design due to communication and comparison across different inventor lineages [66].

[6] When both biased transformation and cultural selection are operating simultaneously (not shown in Fig 4), we see the emergence of transient cultural traditions that accumulate for a while before reverting back to trait X. This results in different trait lineages emerging in the same group over time even in the absence of migration. Even with these simple assumptions, interesting cultural dynamics emerge from the interplay of cultural selection, biased transformation and migration. Readers can explore this at https://amesoudi.shinyapps.io/CSBT_model2/.

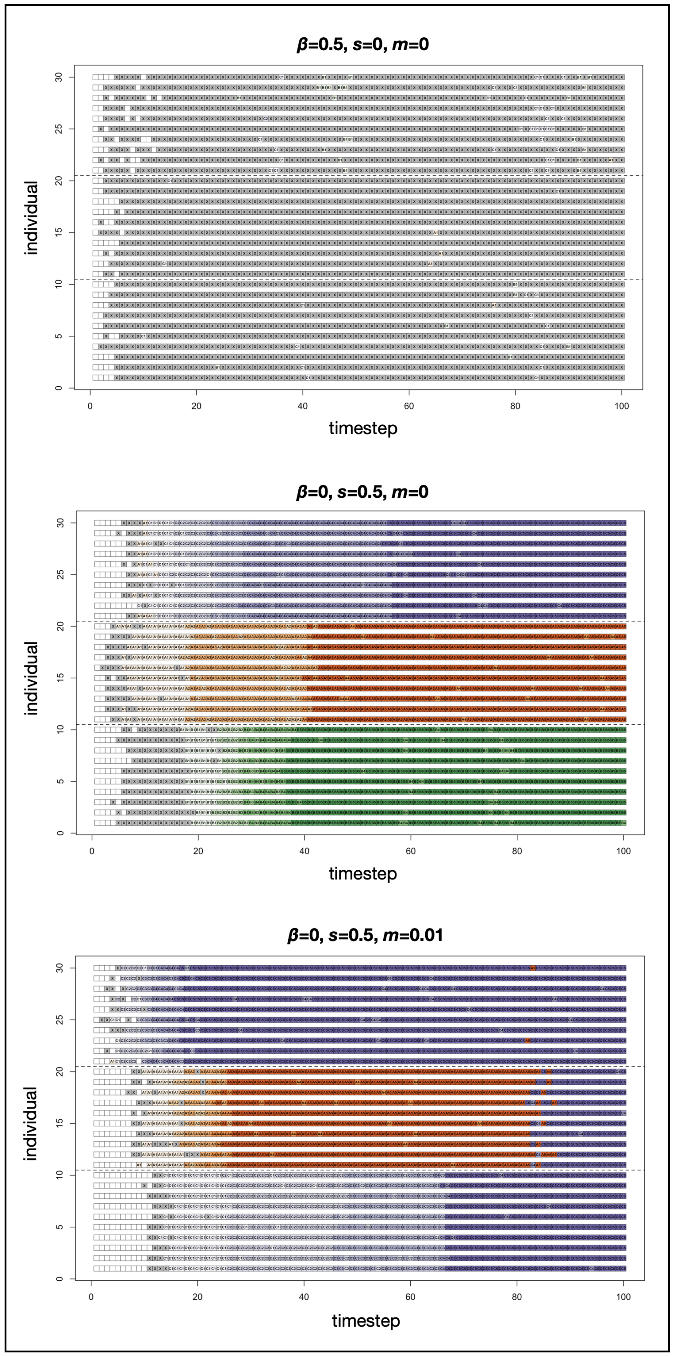

Figure 4: Indicative runs of Model 2. In each plot, each row represents a single individual, and columns represent time-steps. Each row therefore shows how an individual's cultural trait changes over time. Traits are color-coded according to Fig 3, with the intuitive trait X shown in grey, the A lineage in oranges, B lineage in greens and C lineage in purples. The darker the shading, the higher the trait payoff. Individuals are in one of three groups separated with dotted lines, with ten individuals per group. The top plot shows how biased transformation via β generates cross-cultural stability, with each group independently converging on the attractive trait X. The middle plot shows divergence due to cultural selection via s, with each group converging on a different trait lineage. The bottom plot shows convergence on the higest-payoff lineage (C), as migration via m causes C traits to spread to other groups. β = strength of biased transformation, s = probability of cultural selection, m = probability of between-group migration. In all cases, $\sigma = 1$, $n = 10$, $d = 0.5$ and $g = 3$.

Finally, experimental evidence can be used to explore whether a cross-culturally stable cultural trait is attractive or intuitive, e.g. where transmission chains converge on this form, suggesting a role for biased transformation as in [34], or whether the trait is unintuitive, difficult to learn and easily lost, suggesting a role for cultural selection, as in [66]. Such experimental evidence should be conducted cross-culturally and demonstrate that biased transformation acts individually in the same direction in as many of the societies in which it is or has been observed at the population level as possible. If instead the biased transformation dynamic is specific only to certain societies and not others, then biased transformation would be a less likely explanation for cross-cultural stability.

4 General discussion

Cultural evolution is often described as comprising two distinct dynamics: cultural selection and biased transformation. Cultural selection involves small, often undirected modification of cultural traits, followed by the selective copying of certain kinds of individuals or traits. Biased transformation involves the directional modification or transformation of adopted cultural traits often in consistent directions across individuals and societies. These two dynamics are sometimes presented as alternative models for human cultural evolution, and the presence of the latter is sometimes used to argue against the notion that cultural change comprises a Darwinian evolutionary process.

Here I have presented and discussed the results of two simple models in the context of recent empirical work, to try to clarify these issues. Model 1 reinforces the conclusions of previous models [3,42,44,47] that directional change in cultural evolution can be generated by either biased transformation or cultural selection, or both acting together. The two dynamics are not mutually exclusive, and can potentially combine to act in the same direction. Importantly, the presence of directional cultural change alone cannot be taken as evidence for one or the other dynamic. Furthermore, the same psychological mechanisms (e.g. preferences for disgust-eliciting or minimally counter-intuitive information, or a preference for high-payoff outcomes) can potentially underlie directional change generated by both cultural selection and biased transformation. Model 1 also showed that there may be some population-level signatures that can be used to distinguish between the dynamics, specifically the shape of diffusion curves and the effect of population size, but these have limitations.

Similarly, Model 2 illustrates that cross-cultural stability in cultural evolution can be generated by either biased transformation or cultural selection (plus migration), again reflecting previous model results [38,50–52]. Like for directional change, the presence of cross-cultural stability alone cannot be taken as evidence for one or the other. In fact, there are multiple causes of apparent cross-cultural stability: biased transformation due to universal cognitive mechanisms or inductive biases, biased transformation due to individual (e.g. reinforcement) learning in similar ecological conditions, cultural selection due to payoff-biased copying in similar ecological conditions, or cultural selection combined with migration (as in Model 2).

For both directional change and cross-cultural stability, further historical and experimental evidence is needed to identify the dynamics generating that phenomenon. The empirical examples discussed above should indicate that there is evidence for both cultural selection and biased transformation in human cultural evolution. Violin designs [66], given their complexity, opacity and unintuitiveness, have been largely driven by cultural selection, given that the extent of change in each generation is consistent with accidental and undirected mutation due to craftsmanship limitations. The same probably applies to similarly complex and opaque technologies such as glassware [79] and metalworking [80]. In contrast, blood-letting as a medical practice [34], given its intuitive fit with cognitive biases (folk theories of illness), appears to have been largely driven by biased transformation, given experimental evidence that neutral descriptions regularly transform into blood-letting descriptions and the ineffectiveness of blood-letting as a medical practice (ruling out payoff-driven cultural selection). The same probably applies to direct eye gaze in portraits [35] and colour terminologies [36], which similarly reflect intuitive cognitive or perceptual biases.

This suggests that cultural selection and biased transformation may operate on different domains of culture [39]. In those domains where favoured variants are unintuitive or exceed what individual learning alone can produce, such as science, modern technologies or complex socio-political institutions, then cultural selection may be the predominant driver of cultural change. This cultural change becomes cumulative when it exceeds the scope of individual learning [81,82], thus leading to diversification as different populations accumulate different non-intuitive solutions to the same problems (assuming a multimodal fitness landscape, which is a reasonable assumption for domains such as complex technology or socio-political institutions). In those domains where favoured variants are intuitive or within the scope of individual rediscovery (sometimes called the 'zone of latent solutions' [81]), such as artistic traditions, folk tales, folk medicine or food preferences, then biased transformation may be the predominant driver of cultural change. This cultural change is unlikely to be cumulative across generations, and less likely to result in cross-cultural divergence.

The conclusions regarding cross-cultural diversification and cumulative culture drawn from Model 2 depend on the assumptions that there is a single culturally attractive trait (in Model 2 labelled X) that is favoured by biased transformation, and that cultural selection can lead to multiple trait lineages. This seems like a reasonable assumption given empirical case studies to date, each of which find or assume a single attractor, e.g. blood-letting [34], direct eye gaze [35], colour terms consistent with the World Colour Survey [36], linear relationships between variables [32] or symmetrical arrowhead designs [38]. However, where there are different ecological pressures in different areas, then biased transformation may equally generate cross-cultural divergence (for an experimental demonstration of this, see [83]). This is especially likely when biased transformation takes the relatively open-ended and flexible form of individual learning ('guided variation' in [3]), rather than convergence on an ecologically-independent cognitive universal. It is less easy to see how biased transformation can result in cumulative cultural change given that it is, by definition, bounded by individual cognition and learning, and drives cultural traits back to intuitive, simple forms. Nevertheless, distortions arising from biased transformation may serve as variation upon which cultural selection may act, such that biased transformation may play a role in cumulative cultural evolution in combination with cultural selection. Model 2 could be extended to explore these interactions.

A further limitation of the present models is the lack of individual differences in the operation of both cultural selection and biased transformation. Different individuals may employ cultural selection processes such as payoff-biased social learning to different extents, influenced by such factors as cultural background and subsistence [84–86]. In the context of biased transformation, different individuals in the same population may possess different inductive priors (beyond the external ecological differences noted in the previous paragraph), which models show may result in different population-level outcomes to any of those specific individual priors [87].

In conclusion, there should be no debate over whether cultural evolution is characterised by cultural selection or biased transformation: it is characterised by both, weighted differently for different domains, with this weighting being an empirical issue in each case. Whether this justifies calling cultural evolution 'Darwinian' or not depends on how one defines the term 'Darwinian'.[7] While some prefer to restrict the term 'Darwinian' to a selection-only system akin to genetic evolution [44], my preference would be to see genetic and cultural evolution as two different instances of Darwinian evolutionary processes. In cultural evolution, biased transformation is clearly much more important than it is in genetic evolution. But selection is also present. Cultural evolutionists can have the best of both worlds: borrowing tools from biology where appropriate, such as population genetic modelling techniques or phylogenetic methods, but also drawing on cognitive science to study biased transformation-related inductive biases. Focusing on just one of these dynamics seems misguided. For example, focusing solely on biased transformation will obscure the important role of population size and structure on patterns of cultural evolution [60], and ignore the diverging historical cultural lineages that result in cross-cultural variation [82]. On the other hand, focusing solely on cultural selection will downplay the important role of individual cognition and communication in cultural evolution [31], and obscure unique phenomena such as repeated learning and refinement during the lifetime [89,90] that have no precedent in genetic evolution.

[7] Perhaps a minor historical point, but Darwin himself argued that 'use and disuse', by which he meant the Lamarckian-like inheritance of characteristics acquired during an individual's lifetime, played a major role in the evolution of biological species [88]. To the extent that this resembles biased transformation, then given that biased transformation was present in Darwin's original scheme, it is perhaps historically accurate to include biased transformation under the descriptor 'Darwinian' (but not 'neo-Darwinian', after it was shown during the modern synthesis that acquired characteristics are not inherited genetically: [11]).

5 Acknowledgements

I thank Lucas Molleman, Franjo Weissing, Tom Morgan and an anonymous reviewer for valuable comments on an earlier version of this paper.

487 # References

488 1. Wyhe, J. van 2005 The descent of words: Evolutionary thinking 1780-1880. *Endeavour* **29**, 94–100.

489 2. Darwin, C. 1871 *The descent of man.* London: Gibson Square, 2003.

490 3. Boyd, R. & Richerson, P. J. 1985 *Culture and the evolutionary process.* Chicago, IL: Univ. Chicago Press.

491 4. Cavalli-Sforza, L. L. & Feldman, M. W. 1973 Cultural versus biological inheritance: Phenotypic transmission from parents to children. *American Journal of Human Genetics* **25**, 618–637.

492 5. Cavalli-Sforza, L. L. & Feldman, M. W. 1981 *Cultural transmission and evolution.* Princeton: Princeton Univ. Press.

493 6. Youngblood, M. & Lahti, D. 2018 A bibliometric analysis of the interdisciplinary field of cultural evolution. *Palgrave Communications* **4**, 120. (doi:10.1057/s41599-018-0175-8)

494 7. Mesoudi, A. 2017 Pursuing Darwin's curious parallel: Prospects for a science of cultural evolution. *Proceedings of the National Academy of Sciences* **114**, 7853–7860. (doi:10.1073/pnas.1620741114)

495 8. Richerson, P. J. & Christiansen, M. H. 2013 *Cultural evolution: Society, technology, language, and religion.* Cambridge MA: MIT Press.

496 9. Creanza, N., Kolodny, O. & Feldman, M. W. 2017 Cultural evolutionary theory: How culture evolves and why it matters. *Proceedings of the National Academy of Sciences* **114**, 7782–7789. (doi:10.1073/pnas.1620732114)

497 10. Gray, R. D. & Watts, J. 2017 Macro matters: Cultural macroevolution and the prospects for an evolutionary science of human history. *Proceedings of the National Academy of Sciences* **114**, 7846–7852.

498 11. Mesoudi, A. 2011 *Cultural evolution: How Darwinian theory can explain human culture and synthesize the social sciences.* Chicago, IL: University of Chicago Press.

499 12. Mesoudi, A., Whiten, A. & Laland, K. N. 2006 Towards a unified science of cultural evolution. *Behavioral and Brain Sciences* **29**, 329–383. (doi:10.1017/S0140525X06009083)

500 13. Muthukrishna, M. & Henrich, J. 2019 A problem in theory. *Nature Human Behaviour*, 1. (doi:10.1038/s41562-018-0522-1)

501 14. Henrich, J. 2015 *The secret of our success.* Princeton University Press.

502 15. Richerson, P. J. & Boyd, R. 2005 *Not by genes alone.* Chicago: Univ. Chicago Press.

503 16. Henrich, J. & McElreath, R. 2003 The evolution of cultural evolution. *Evolutionary Anthropology* **12**, 123–135. (doi:10.1002/evan.10110)

504 17. Cavalli Sforza, L. L., Feldman, M. W., Chen, K. ho & Dornbusch, S. M. 1982 Theory and observation in cultural transmission. *Science* **218**, 19–27.

505 18. Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. J. H., Webster, M. M. & Laland, K. N. 2011 Cognitive culture: Theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences* **15**, 68–76. (doi:10.1016/j.tics.2010.12.002)

506 19. Kendal, R. L., Boogert, N. J., Rendell, L., Laland, K. N., Webster, M. & Jones, P. L. 2018 Social learning strategies: Bridge-building between fields. *Trends in Cognitive Sciences* (doi:10.1016/j.tics.2018.04.003)

507 20. Herrmann, E., Call, J., Hernandez-Lloreda, M. V., Hare, B. & Tomasello, M. 2007 Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science* **317**, 1360–1366.

508 21. Laland, K. N. 2017 *Darwin's unfinished symphony: How culture made the human mind.* Princeton University Press.

509 22. Boyd, R., Richerson, P. J. & Henrich, J. 2011 The cultural niche. *Proceedings of the National Academy of Sciences* **108**, 10918–10925.

510 23. Derex, M., Bonnefon, J.-F., Boyd, R. & Mesoudi, A. 2019 Causal understanding is not necessary for the improvement of culturally evolving technology. *Nature Human Behaviour* **3**, 446–452. (doi:10.1038/s41562-019-0567-9)

511 24. Henrich, J. & Henrich, N. 2010 The evolution of cultural adaptations: Fijian food taboos protect against dangerous marine toxins. *Proceedings of the Royal Society B* **277**, 3715–3724.

512 25. Derex, M., Beugin, M.-P., Godelle, B. & Raymond, M. 2013 Experimental evidence for the influence of group size on cultural complexity. *Nature* **503**, 389–391.

513 26. Beheim, B. A., Thigpen, C. & McElreath, R. 2014 Strategic social learning and the population dynamics of human behavior: The game of Go. *Evolution and Human Behavior* **35**, 351–357. (doi:10.1016/j.evolhumbehav.2014.04.001)

514 27. Atran, S. 2001 The trouble with memes: Inference versus imitation in cultural creation. *Human Nature* **12**, 351–381.

515 28. Boyer, P. 1998 Cognitive tracks of cultural inheritance: How evolved intuitive ontology governs cultural transmission. *American Anthropologist* **100**, 876–889.

516 29. Claidière, N., Scott-Phillips, T. C. & Sperber, D. 2014 How Darwinian is cultural evolution? *Philosophical Transactions of the Royal Society B* **369**, 20130368. (doi:10.1098/rstb.2013.0368)

517 30. Scott-Phillips, T., Blancke, S. & Heintz, C. 2018 Four misunderstandings about cultural attraction. *Evolutionary Anthropology: Issues, News, and Reviews* **27**, 162–173. (doi:10.1002/evan.21716)

518 31. Sperber, D. 1996 *Explaining culture: A naturalistic approach.* Oxford: Oxford University Press.

519 32. Griffiths, T. L., Kalish, M. L. & Lewandowsky, S. 2008 Theoretical and empirical evidence for the impact of inductive biases on cultural evolution. *Philosophical Transactions of the Royal Society B* **363**, 3503–3514.

520 33. Kalish, M. L., Griffiths, T. L. & Lewandowsky, S. 2007 Iterated learning: Intergenerational knowledge transmission reveals inductive biases. *Psychonomic Bulletin and Review* **14**, 288–294.

521 34. Miton, H., Claidière, N. & Mercier, H. 2015 Universal cognitive mechanisms explain the cultural success of bloodletting. *Evolution and Human Behavior* **36**, 303–312. (doi:10.1016/j.evolhumbehav.2015.01.003)

522 35. Morin, O. 2013 How portraits turned their eyes upon us: Visual preferences and demographic change in cultural evolution. *Evolution and Human Behavior* **34**, 222–229. (doi:10.1016/j.evolhumbehav.2013.01.004)

523 36. Xu, J., Dowman, M. & Griffiths, T. L. 2013 Cultural transmission results in convergence towards colour term universals. *Proceedings of the Royal Society B: Biological Sciences* **280**.

524 37. Kirby, S., Cornish, H. & Smith, K. 2008 Cumulative cultural evolution in the laboratory: An experimental approach to the origins of structure in human language. *Proceedings of the National Academy of Sciences* **105**, 10681–10686.

525 38. Thompson, B. & Griffiths, T. L. 2019 Inductive biases constrain cumulative cultural evolution.

526 39. Acerbi, A. & Mesoudi, A. 2015 If we are all cultural Darwinians what's the fuss about? Clarifying recent disagreements in the field of cultural evolution. *Biology and Philosophy* **30**, 481–503. (doi:10.1007/s10539-015-9490-2)

527 40. Buskell, A. 2017 What are cultural attractors? *Biology & Philosophy* **32**, 377–394. (doi:10.1007/s10539-017-9570-6)

528 41. El Mouden, C., André, J.-B., Morin, O. & Nettle, D. 2014 Cultural transmission and the evolution of human behaviour: A general approach based on the Price equation. *Journal of Evolutionary Biology* **27**, 231–241. (doi:10.1111/jeb.12296)

529 42. Henrich, J. & Boyd, R. 2002 On modeling cognition and culture: Why cultural evolution does not require replication of representations. *Journal of Cognition and Culture* **2**, 87–112.

530 43. Aguilar, E. G. & Akçay, E. 2018 Gene-culture coinheritance of a behavioral trait. *The American Naturalist* **192**, 311–320. (doi:10.1086/698872)

531 44. Nettle, D. 2020 Selection, adaptation, inheritance and design in human culture: The view from the Price equation. *Philosophical Transactions of the Royal Society B: Biological Sciences* **375**, 20190358. (doi:10.1098/rstb.2019.0358)

532 45. Price, G. R. 1970 Selection and covariance. *Nature* **227**, 520–521.

533 46. Gardner, A. 2020 Price's equation made clear. *Philosophical Transactions of the Royal Society B: Biological Sciences* **375**, 20190361. (doi:10.1098/rstb.2019.0361)

534 47. Claidière, N. & Sperber, D. 2007 The role of attraction in cultural evolution. *Journal of Cognition and Culture* **7**, 89–111.

535 48. Claidière, N. & André, J.-B. 2012 The transmission of genes and culture: A questionable analogy. *Evolutionary Biology* **39**, 12–24. (doi:10.1007/s11692-011-9141-8)

536 49. Smaldino, P. E. 2016 Models are stupid, and we need more of them. In *Computational Models in Social Psychology* (eds R. R. Vallacher A. Nowak & S. J. Read), Psychology Press.

537 50. Acerbi, A., Charbonneau, M., Miton, H. & Scott-Phillips, T. 2019 Cultural stability without copying. (doi:10.31219/osf.io/vjcq3)

538 51. Mesoudi, A. 2018 Migration, acculturation, and the maintenance of between-group cultural variation. *PLOS ONE* **13**, e0205573. (doi:10.1371/journal.pone.0205573)

539 52. Morgan, T. J. H. 2016 Testing the cognitive and cultural niche theories of human evolution. *Current Anthropology* **57**, 370–377. (doi:10.1086/686531)

540 53. Garbett, S. & Kozdoba, M. 2020 Emg: Exponentially Modified Gaussian (EMG) Distribution.

541 54. Newberry, M. G., Ahern, C. A., Clark, R. & Plotkin, J. B. 2017 Detecting evolutionary forces in language change. *Nature* **551**, 223–226. (doi:10.1038/nature24455)

542 55. Henrich, J. 2001 Cultural transmission and the diffusion of innovations. *American Anthropologist* **103**, 992–1013.

543 56. Rogers, E. 1995 *The diffusion of innovations*. New York: Free Press.

544 57. Lefebvre, L. 1995 Culturally transmitted feeding behaviour in primates: Evidence for accelerating learning rates. *Primates* **36**, 227–239.

545 58. Reader, S. M. 2004 Distinguishing social and asocial learning using diffusion dynamics. *Learning and Behavior* **32**, 90–104.

546 59. Hoppitt, W., Kandler, A., Kendal, J. R. & Laland, K. N. 2010 The effect of task structure on diffusion dynamics: Implications for diffusion curve and network-based analyses. *Learning & Behavior* **38**, 243–251. (doi:10.3758/LB.38.3.243)

547 60. Derex, M. & Mesoudi, A. 2020 Cumulative cultural evolution within evolving population structures. *Trends in Cognitive Sciences* (doi:10.1016/j.tics.2020.04.005)

548 61. Henrich, J. 2004 Demography and cultural evolution. *American Antiquity* **69**, 197–214.

549 62. Henrich, J., Boyd, R., Derex, M., Kline, M. A., Mesoudi, A., Muthukrishna, M., Powell, A. T., Shennan, S. J. & Thomas, M. G. 2016 Understanding cumulative cultural evolution. *Proceedings of the National Academy of Sciences* **113**, E6724–E6725. (doi:10.1073/pnas.1610005113)

550 63. Vaesen, K., Collard, M., Cosgrove, R. & Roebroeks, W. 2016 Population size does not explain past changes in cultural complexity. *Proceedings of the National Academy of Sciences* **113**, E2241–E2247. (doi:10.1073/pnas.1520288113)

551 64. Kline, M. A. & Boyd, R. 2010 Population size predicts technological complexity in Oceania. *Proceedings of the Royal Society B* **277**, 2559–2564.

552 65. Acerbi, A., Kendal, J. & Tehrani, J. J. 2017 Cultural complexity and demography: The case of folktales. *Evolution and Human Behavior* **38**, 474–480. (doi:10.1016/j.evolhumbehav.2017.03.005)

553 66. Nia, H. T., Jain, A. D., Liu, Y., Alam, M.-R., Barnas, R. & Makris, N. C. 2015 The evolution of air resonance power efficiency in the violin and its ancestors. *Proceedings of the Royal Society of London A* **471**, 20140905. (doi:10.1098/rspa.2014.0905)

554 67. Heyes, C. & Pearce, J. M. 2015 Not-so-social learning strategies. *Proceedings of the Royal Society B* **282**, 20141709. (doi:10.1098/rspb.2014.1709)

555 68. Mesoudi, A. & Whiten, A. 2008 The multiple roles of cultural transmission experiments in understanding human cultural evolution. *Philosophical Transactions of the Royal Society B* **363**, 3489–3501.

556 69. Eriksson, K. & Coultas, J. C. 2014 Corpses, maggots, poodles and rats: Emotional selection operating in three phases of cultural transmission of urban legends. *Journal of Cognition and Culture* **14**, 1–26. (doi:10.1163/15685373-12342107)

557 70. Heath, C., Bell, C. & Sternberg, E. 2001 Emotional selection in memes: The case of urban legends. *Journal of Personality and Social Psychology* **81**, 1028–1041. (doi:10.1037/0022-3514.81.6.1028)

558 71. Griffiths, T. L., Christian, B. R. & Kalish, M. L. 2008 Using categorical structures to test iterated learning as a method for identifying inductive biases. *Cognitive Science* **32**, 68–107.

559 72. Mesoudi, A., Whiten, A. & Dunbar, R. 2006 A bias for social information in human cultural transmission. *British Journal of Psychology* **97**, 405–423. (doi:10.1348/000712605X85871)

560 73. Stubbersfield, J. M., Tehrani, J. J. & Flynn, E. G. 2014 Serial killers, spiders and cybersex: Social and survival information bias in the transmission of urban legends. *British Journal of Psychology* **106**, 288–307. (doi:10.1111/bjop.12073)

561 74. Barrett, J. L. & Nyhof, M. A. 2001 Spreading non-natural concepts: The role of intuitive conceptual structures in memory and transmission of cultural materials. *Journal of Cognition and Culture* **1**, 69–100.

562 75. Bebbington, K., MacLeod, C., Ellison, T. M. & Fay, N. 2017 The sky is falling: Evidence of a negativity bias in the social transmission of information. *Evolution and Human Behavior* **38**, 92–101. (doi:10.1016/j.evolhumbehav.2016.07.004)

563 76. Fessler, D. M. T., Pisor, A. C. & Navarrete, C. D. 2014 Negatively-biased credulity and the cultural evolution of beliefs. *PLoS ONE* **9**. (doi:10.1371/journal.pone.0095167)

564 77. Derex, M. & Boyd, R. 2016 Partial connectivity increases cultural accumulation within groups. *Proceedings of the National Academy of Sciences* **113**, 2982–2987. (doi:10.1073/pnas.1518798113)

565 78. Derex, M., Perreault, C. & Boyd, R. 2018 Divide and conquer: Intermediate levels of population fragmentation maximize cultural accumulation. *Phil. Trans. R. Soc. B* **373**, 20170062. (doi:10.1098/rstb.2017.0062)

566 79. Macfarlane, A. & Martin, G. 2002 *Glass: A world history.* University of Chicago Press.

567 80. Inoue, T. 2010 Tatara and the Japanese sword: The science and technology. *Acta mechanica* **214**, 17–30.

568 81. Tennie, C., Call, J. & Tomasello, M. 2009 Ratcheting up the ratchet: On the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B* **364**, 2405–2415.

569 82. Mesoudi, A. & Thornton, A. 2018 What is cumulative cultural evolution? *Proceedings of the Royal Society B* **285**, 20180712. (doi:10.1098/rspb.2018.0712)

570 83. Miton, H., Wolf, T., Vesper, C., Knoblich, G. & Sperber, D. 2020 Motor constraints influence cultural evolution of rhythm. *Proceedings of the Royal Society B: Biological Sciences* **287**, 20202001. (doi:10.1098/rspb.2020.2001)

571 84. Mesoudi, A., Chang, L., Dall, S. R. X. & Thornton, A. 2016 The evolution of individual and cultural variation in social learning. *Trends in Ecology and Evolution* **31**, 215–225. (doi:10.1016/j.tree.2015.12.012)

572 85. Molleman, L., Berg, P. van den & Weissing, F. J. 2014 Consistent individual differences in human social learning strategies. *Nature Communications* **5**. (doi:10.1038/ncomms4570)

573 86. Glowacki, L. & Molleman, L. 2017 Subsistence styles shape human social learning strategies. *Nature Human Behaviour* **1**, 0098. (doi:10.1038/s41562-017-0098)

574 87. Navarro, D. J., Perfors, A., Kary, A., Brown, S. D. & Donkin, C. 2018 When extremists win: Cultural transmission via iterated learning when populations are heterogeneous. *Cognitive Science* **42**, 2108–2149. (doi:https://doi.org/10.1111/cogs.12667)

575 88. Darwin, C. 1859 *The origin of species.* London: Penguin, 1968.

576 89. Morin, O. 2015 *How traditions live and die.* Oxford University Press.

90. Strimling, P., Enquist, M. & Eriksson, K. 2009 Repeated learning makes cultural evolution unique. *Proceedings of the National Academy of Sciences* **106**, 13870–13874.