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Homology Across Inheritance Systems

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1. Introduction

One might think that if a character resemblance between two lineages is transmitted through different channels of inheritance – e.g., genes in one case and culture in the other – then it cannot be the result of common ancestry. The assumption that homologies cannot cross inheritance systems has framed anthropological debates regarding the phylogeny of complex cognitive and behavioural resemblances between humans and common chimpanzees, with differences in developmental acquisition taken to imply disparate phylogenetic origins (Maestripieri and Roney 2006; Marks 2003; Wrangham and Peterson 1996). In this paper we reject the assumption that any character resemblance that is culturally transmitted in one species but genetically transmitted in another closely related species is necessarily or even probably non-homologous between them.

We argue that since homology relations can be preserved despite a change in developmental mechanisms (§2), they could in principle be preserved across a change in inheritance system, even on a stringent account of what it takes to qualify as an inheritance system (§3), so long as the trait has been continuously transmitted in a lineage. Then we turn to cultural transmission in particular, arguing that it can support phenotypic lineages and hence homology relations (§4). We go on to describe two scenarios in which homology can cross between genetic and cultural inheritance systems (the processes of genetic and cultural assimilation) (§5), and briefly consider whether our points carry over to developmental accounts of homology (§6). Finally we set out the implications of this discussion for debates over the phylogeny of similar character states in humans and chimpanzees, using intergroup violence as an illustration (§7).

2. Homology Across Change in Developmental Resources

Reconstructing patterns of evolutionary descent has been one of the central preoccupations of biology ever since Darwin sketched the first proto-cladogram in his early notebooks. Identifying homologs is crucial to reconstructing phylogenetic relationships and delineating monophyletic taxa. On standard phylogenetic accounts of homology, a similar character state found in two different lineages is homologous just in case it was present in and inherited continuously from their common ancestor.[1] Here we adopt this 'taxic' homology concept. To

[1] This paper does not take a stand on the general 'problem of homology.' Instead, we will simply stipulate that by 'homology' we mean 'taxic homology' which we define, broadly following Wiley and

accommodate 'transformational homologs' (traits that correspond to, but fail to structurally resemble, one another), 'serial homologs' (e.g., digits or segments within an organism that do not share a phylogenetic history), and ancestor-descendant sequences, biologists and philosophers of science have offered non-genealogical accounts of homology grounded in mechanism and couched either in terms of shared developmental constraints or continuity of informational resources involved in development. We will return at the end (§6) to consider whether our claims extend to, and perhaps pose problems for, non-taxic conceptions of homology.

It is clear from work in evolutionary developmental biology that we cannot infer from the fact that a shared character state is produced by different developmental mechanisms in distinct lineages that it is non-homologous between them (Wagner 2007; Hall 2003). It is true that a difference in developmental mechanisms *can* be evidence against homology. For instance, there are fundamental differences in the developmental patterning of camera-type eyes in cephalopods and vertebrates, which almost certainly reflect the fact that the last common ancestor did not possess the trait. However, evolutionary continuity in morphological structures can survive very substantial change in the developmental mechanisms by which those structures are realised in embryogenesis.

The unexpected resilience of phenotypes across genetic perturbations is now extensively documented (de Visser et al. 2003). This flexibility allows that, over evolutionary time, different suites of genes may become involved in the development of the same structure, which is conserved in distant taxa by stabilising selection (Roth 1991). Weiss and Fullerton (2000) have described such genetic turnover as 'phenogenetic drift', while Müller (2003) has referred to the same phenomenon as the 'autonomization' of the phenotype. A second type of developmental turnover relates to embryological precursors and patterning mechanisms that underwrite what are regarded, for independent reasons, as homologous traits (Roth 1988/2001). This developmental variability characterizes early stages of embryogenesis such as cleavage, gastrulation and neural tube formation (Rieppel 1992), as well as the patterning of vertebrate limb buds and insect segmentation (Pigliucci 2010).

In sum, a character that has arisen only once may be preserved in a clade despite substantial variation, or even a complete turnover, in its underlying developmental generators (Fig.1). This phenomenon of developmental turnover illustrates a more general point about homology, namely that homology assessments are relative to a particular grain of analysis—a point that has been made forcefully by Hall (2003, 416). Homology at one level of description, such as morphology or behavior, need not entail homology at other levels, such as developmental, genetic or neuro-cognitive processes.

[INSERT FIGURE 1 HERE]

Lieberman (2011), as 'character states that are shared by two taxa and inherited continuously from their common ancestor'. In contrast, 'homoplasy' will refer to qualitatively similar character states that do not stem from a common ancestor (and hence diagnose polyphyletic groups). Our focus is therefore on the homology of *similar character states*, rather than on individuated *characters* whatever their state.

While the reality of developmental turnover may be widely appreciated in the 'evo devo' literature, these crucial lessons have yet to percolate into mainstream evolutionary anthropology and comparative ethology, where researchers continue to adhere to 'mechanistic' assumptions in relation to homology. For instance, in considering the possibility of homology between human and nonhuman animal behavioral traits, Maestripieri and Roney (2006, 125) hold that "homologous traits have, by definition, a common phylogenetic history *and are produced by similar developmental processes*," (emphasis added). They cite the biological homology concept (see §7) in support of the assumption that homology implies similar developmental mechanisms. Likewise, skeptics of behavioral homology ascriptions between human and non-human primates, such as Gottlieb and Lickliter (2004, 317), hold that "homologies in two or more species are presumed to be evolutionarily derived from a common ancestor, implying common genetic and other developmental components that were present in the ancestor and result in the formal similarity of behavior in their descendants."

These mechanistic assumptions have infected methodology and inferential reasoning in evolutionary psychology. For instance, evolutionary psychologists in the nativist tradition often appeal to the taxonomic distribution of a trait (e.g., a putative moral emotion) to support their proffered theory regarding its developmental acquisition in humans. More specifically, such theorists look for the presence of a proto version of the trait in closely related but weakly cultural taxa (such as chimps or other non-human primates), assume that the proto trait and full-fledged trait are homologs, and then infer from this homologous relation that the trait is a conserved, gene-based adaptation that is 'innate' and/or rooted in 'human nature' rather than culturally acquired in humans (for a critical discussion of this approach, see Prinz 2008).

For reasons we shall see, the biological homology concept and similar mechanistic approaches to homology can lead to significant confusions when applied to the phylogeny of complex behavioral adaptations, which are frequently and problematically set in opposition to traits that develop via enculturation (for an example of this framing, see Maestripieri and Roney 2006, 131). Furthermore, shifts from the genetic to cultural inheritance system entail a more extreme phenotypic decoupling from underlying developmental constraints and even the broader genetic substrate than has been contemplated in the 'developmental turnover' literature. Thus, while our thesis is particularly relevant to evolutionary psychology and anthropology, it is also of wider biological significance.

3. Homology Across Inheritance Systems in Principle

Even if homologies can survive some changes in developmental resources, they still require descent—that is, the continuous transmission of the trait in different lineages. Homology is only maintained because the factors that cause a phenotypic similarity between parents and offspring are transmitted down the generations. One might think then that these factors cannot change drastically without disrupting the homology relation. In this section we argue that, surprisingly, homologies can subsist across differences in the inheritance mechanisms

responsible for transmitting traits down the generations. That possibility can only be assessed given an account of what it is for a trait to be transmitted by a particular inheritance system. This section sets out one such account and shows that it allows for a homologous trait to be transferred from one inheritance system to another.

According to a popular but erroneous view of development, genes program, blueprint or otherwise causally determine particular phenotypic outcomes. If this were right, then the sort of evolutionary change described above in the genetic resources involved in the development of a continuously transmitted trait could include a change in the genes that program or control development of that trait. Similarly, control could be handed over from genetic programs to epigenetic or cultural determinants, or vice versa. Unfortunately for this neat account, the picture of genes as the locus of special causal agency in development is mistaken (Oyama 2000; Griffiths 2001; Robert 2004; Pigliucci 2010; Bertossa 2011). Genes are one amongst many causal factors that make a contingent difference to organismic development (Oyama 2000). Without specific details about the developmental system in question, there is no basis to say that genes are inherently privileged as a class of causes relative to other developmental factors. Genetic differences have a causal influence on phenotypic outcomes or bias development in particular directions in just the same way that epigenetic, environmental and cultural factors do.

Despite having no special causal status in development, genes do of course have a special evolutionary role, since they are developmental difference-makers that are reliably transmitted down the generations, so that selection can act on the phenotypic differences they produce. Furthermore, there is evidence that DNA and its mechanisms of replication, repair and expression have been selected to perform this function (Freeland and Hurst 1998). We will refer to any mechanism that has been selected to perform the function of transmitting phenotypes[2] down the generations as an *inheritance system* (Shea 2007). This is a meta-function that is additional to the functions of particular genes to produce the particular phenotypes for which they have been selected. An inheritance system transmits down the generations a 'resource' (a genetic variant, epigenetic mark, behavioural variant, etc.), which biases the production of a particular developmental outcome on which natural selection can then act.

In addition to DNA, epigenetic systems that stably transmit variants over many generations may also have been selected for the meta-function of transmitting phenotypes down the generations (Shea, Pen and Uller 2011). Any such mechanism thereby also qualifies as an inheritance system. Similarly, some mechanisms of cultural learning and transmission may have been selected for their ability to transmit phenotypes down the generations (Shea 2009), in which case such cultural mechanisms too will constitute an inheritance system. In either case, it is a very stringent test. Environmental factors that are causally important in development, even if they persist or recur reliably in each generation, are not normally transmitted down the generations by a system with the function of transmitting phenotypes

[2] We use the term 'phenotype' in the broad, 'extended' sense to include not only quintessential biological structures but also behaviors, mental representations, and artifacts.

down the generations, so they will not count as an inheritance system on this test. Likewise, developmental changes that are subsequently stabilised by selection on genes (West-Eberhard 2003) illustrate the general point of developmental turnover, but do not in themselves exemplify a change in inheritance systems since the initial developmental change need not be transmitted by an inheritance system at all (see also §5.1).

In one sense, the claim that homology can be preserved across inheritance systems follows straightforwardly from, and is a special case of, the more general claim that homology can survive across changes in developmental resources, some of which will be inherited from parent to offspring. We think this logical extension is an interesting and underappreciated result. While genetic, epigenetic, environmental and cultural developmental factors may be to some degree interchangeable, homology can only survive a complete shift to a new developmental resource if phenotypic similarity is reliably passed down the generations, as this is a necessary condition for sustaining homology relations. If genes are the only developmental resources that are transmitted by an inheritance system, then homologies will remain tightly if not inextricably linked to genes. If, on the other hand, there are non-genetic inheritance systems, then homologies may be preserved even when the genes on the basis of which a trait was selected are no longer involved in their development.

What would it be for a phenotype transmitted initially by one inheritance system to be picked up and transmitted by a different inheritance system? For instance, what would it be for an adaptation P selected on the basis of stably transmitted epigenetic variants to come to be transmitted by the genetic inheritance system? For that to happen, it would not be enough that genes are *causally involved* in the development of P, nor even that additional genes become causally involved in the development of P. The genetic inheritance system would only acquire a role in transmitting P if there were relevant phenotypic variation (P vs. some different phenotype P') caused by a genetic difference (G vs. G'), and the fitter genetic variant was selected in virtue of its correlation with P. That is, selection on genetic differences with respect to P would make P at least a partial gene-based adaptation, even if it had initially been selected in virtue of epigenetic variation. Thus, a trait that was initially transmitted by an epigenetic inheritance system can come to be transmitted by the genetic inheritance system as well.

It would be enough for our point about homology to observe that a trait initially transmitted by one inheritance system can come to be transmitted by two systems simultaneously. However, we should also note that a complete transfer between inheritance systems is also possible, due to the kind of change in developmental resources described in the last section. Reprising our example, once P has come to be genetically transmitted (in the sense defined above), alternative causal routes to the development of P may be available that do not rely on the epigenetic mark in virtue of which P was originally selected. If that original epigenetic variant loses its causal role in the development of P, then P is no longer being transmitted by the epigenetic inheritance system, but now only by the genetic inheritance system, and transfer between inheritance systems is complete. We take no stance on whether such complete transfer is likely to occur in real cases, restricting ourselves to noting its possibility.

Below we will assess the possibility that a culturally transmitted phenotype could come to be transmitted by the genetic inheritance system, and the converse. To do this, however, we first need to show that phenotypic features whose development depends heavily on cultural resources can indeed be the subject of homology relations.

4. Homology in Cultural Evolution

Our theortical point about the possibility of homology crossing inheritance systems holds regardless of whether culture in fact forms an inheritance system that supports homology relations. However, if culture were plausibly an inheritance system that supports homology relations, and if homology can indeed cross inheritance systems, this would add significant force to our critcisms of the ways in which theorists have reasoned with the homology concept in disputes over the phylogeny of complex behavioral traits shared between humans and other primates (§§2,7).

Crucially, homology is not limited to structural morphology and its genetic-developmental underpinnings. Behaviour, which is often evolutionarily conserved, is also a proper subject of homology relations and can be used in phylogenetic reconstruction (Rendall and Di Fiore 2007; Bertossa 2011; Hall 2013). Although behavior is developmentally labile, dependent on environmental input, and realized via disparate ontogenetic pathways, the same holds true of morphology, and thus these properties do not preclude its 'homologization'. If we can homologize genetically transmitted behaviors, why should we not be able to do the same with respect to culturally transmitted traits?

Cultural transmission has a number of properties that might give rise to scepticism regarding its ability to support homology relations. To appreciate the difficulties that arise in attempting to extend the homology concept into the cultural context, it is useful to contrast the patterns and processes of genetic and cultural evolution. The phylogenetic reconstruction of eukaryotic taxa is possible because there is little significant genetic exchange between disparate branches of the eukaryotic tree of life, resulting in a strong signal of vertical inheritance that anchors the reconstruction of plant and animal phylogenies. What emerges from this process is a bifurcating macroevolutionary pattern that is amenable to cladistic analysis.[3] Applying cladistics to culture is more controversial because modes of cultural inheritance depart significantly from the digital replication and vertical transmission exemplified by genetic transmission in eukaryotes.

Non-vertical transmission in culture is analogous to lateral gene transfer in prokaryotes, since it allows for the movement of developmental difference-makers across distantly related lineages. Unlike the 'hard heredity' associated with genetic replication, cultural transmission involves teaching, learning, and imitation, with variants acquired and

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[3] Animal taxa have been subject to a non-trivial amount of lateral gene exchange mediated by viral vectors (Keeling and Palmer 2008), and hybridization between disparate plant species may occur at an evolutionarily significant frequency, but these phenomena are not substantial enough to undermine the project of using DNA to build phylogenetic trees in eukaryotes.

lost within the lifetime of an organism. Moreover, vertical (parent-offspring) relations among cultural variants become attenuated as individuals intelligently infer, manipulate, and transform them, amalgamating cultural items from disparate social sources (Sperber 1996). These factors make it less likely that culture will form discrete lineages. Nevertheless, there are strong indications that cultural systems can evolve through a process of descent with modification, suggesting that gene-like replication at the organism level is not a precondition for cumulative cultural evolution and the phylogenetic reconstruction thereof.

Firstly, some of the ostensible difficulties for homology that arise in connection with non-vertical modes of inheritance can be overcome by adopting a coarser grain of analysis. In a recent paper on adaptationism, Wilkins and Godfrey-Smith (2009) argue persuasively that a proper description of the evolutionary mechanisms operating on a population depends on our perspectival grain of analysis. From a 'zoomed-in' perspective of the cultural adaptive landscape, we see non-vertical transmission, intelligent manipulation of variation, inference-generated noise and other dynamics that tend to obscure lineage-like cultural relations. From a more zoomed-out grain of resolution, however, corresponding to what Godfrey-Smith (2013) calls the 'meso-evolutionary' level, we see a discrete network of populations exhibiting local cultural variation. The meso-evolutionary perspective reveals selective processes acting on stable differences between coherent cultural groups, notwithstanding the non-replicative nature of individual-level cultural transmission. The upshot is that token cultural copying is not necessary to generate population-level homology relations.

Secondly, work over the last two decades on cultural evolution has shown that distributed information structures and essentially content-neutral copying biases can allow for the accumulation of fitness-enhancing cultural variation at the population-level, despite the noise and parasite threat associated with non-vertical, inference-modulated cultural transmission (Richerson and Boyd 2005). These models indicate that cultural variants need not be replicated from individual to individual, so long as members of a cultural group are biased toward copying successful strategies and are capable of assimilating characteristics of the population as a distributed whole (Henrich et al. 2008; Laland and Brown 2011).

These theoretical considerations suggest that cultural evolution may operate as a broadly Darwinian process at the population level even in the absence of individual-based lineages of transmission (Godfrey-Smith 2009). The key empirical issue is whether cultures remain sufficiently isolated to sustain distinct traditions that are not swamped by variation flowing in from adjacent cultural groups (Boyd et al. 1997). A growing body of empirical work has succeeded in reconstructing culture-based phylogenetic trees. For a wide range of cultural traits, phylogeny turns out to be a stronger predictor of similarity than geography, painting an increasingly lineage-based rather than diffusion-based picture of cultural evolution. Cultural lineages have been identified (and genetically corroborated) for traits such as subsistence innovations, house-constructing techniques, family and marriage structures, sexual division of labour, metal-working technologies (for a review, see Mace and Jordon 2011), canoe-design (Rogers, Feldman and Ehrlich 2009), projectile points (Buchanan and Collard, 2007), textile designs (Tehrani and Collard 2002), languages (Gray et al. 2009), semantic distinctions (Jordan 2011) and lexical replacements (Pagel 2009). Moreover, as

these methods have been successfully applied to post-Neolithic human populations with sophisticated methods of subsistence, communication, trade and transportation, it is likely that they would be equally if not more applicable to the smaller hunter-gatherer groups of earlier hominin evolution, which were more insulated from other cultures and hence likely to exhibit less intercultural blending.

In sum, although culturally transmitted phenotypes may not follow clean lines of descent connecting discrete individuals at the micro-level, in a broad range of cases cultural evolution exhibits a tree-like signal that is not washed out by intercultural blending. In this context it is legitimate to ask whether a given trait was present and inherited continuously in a given cultural lineage. Thus the homology concept can be applied to traits that are the result of cultural evolution. For example, two cultures may show similarities and differences in the phonetics of the words used in a common basic vocabulary. The homology question relates to whether the similarities are due to common descent. Given enough dimensions of comparison and the absence of strong external constraints, there can be convincing evidence that the similarities were present in the last common cultural ancestor and have been inherited continuously in each lineage ever since.

5. Homology Across Genetic-Cultural Inheritance Systems

In this section we investigate the possibility that homology could subsist across a change from genetic to cultural transmission, and vice versa.

5.1 Change in Developmental Resources vs. Change in Inheritance Systems

A trait whose development relies to a great extent on cultural factors in one lineage can be homologous to a similar trait in another lineage that develops in the absence of, or is insensitive to, cultural factors. For example, development of normal skin structure depends on vitamin C. Production in vivo in other mammals has been replaced in primates by ingestion in the diet. Modern industrialized humans have shifted further, to depend very heavily on culture for dietary vitamin C (farmed fruit, supermarket supply chains, vitamin fortifications and supplements, etc.). Genes allowing for the physiological synthesis of vitamin C have mutated to dysfunction in primates, and in humans cultural factors have come to play an essential causal role in traits like skin structure that depend on vitamin C. The increased causal role of culture in humans does not prevent the basic features of skin structure and physiology shared between humans, primates (some asocial) and other mammals from being homologous. This is merely a further example of change in developmental mechanisms, as discussed in §2. The more difficult question for this section is whether transmission of a homologous trait can transfer between genetic and cultural *inheritance systems*.

In §3 we introduced a tightly delineated notion of what it is to be an inheritance system. An inheritance system is a mechanism with the meta-function of transmitting phenotypes down the generations. Acquiring such a meta-function is a very substantial hurdle. It is not enough that the mechanism happens to be a locus of heritable phenotypic

variation, as may be the case to a limited extent with, for example, the template-based copying of cell membrane structures (Jablonka and Lamb 2005).[4] There must have been selection for the capacity of the mechanism to transmit phenotypes over many generations, as suggested in the case of DNA by the existence of proofreading and repair mechanisms.[5] Culture could support phylogenies in the ways set out in the previous section without constituting an inheritance system in this strict sense.

Transfer of transmission between genetic and cultural inheritance systems trivially requires that there are one or more cultural inheritance systems. That is an empirical issue that remains unresolved, since no one has to our knowledge shown definitively that culture has the requisite meta-level function (§4).[6] Our primary point is that, if there are cultural inheritance systems, then homologies can cross the boundary between genetic and cultural inheritance systems. We do, however, find it plausible that some aspects of culture may have the requisite meta-function. For example, the peculiar way humans, but not other apes, 'overimitate' when learning complex behavioural sequences (instead of performing the behavioural sequence that would be most efficient by rational lights) would be explicable if it is an adaptation for the high-fidelity transmission of behavioural phenotypes (Shea 2009). Moreover, the fact that culture is capable of supporting homology relations (§4) could be taken to support the inference that it has been evolutionarily designed for the transmission of adaptive variants down the generations, although byproduct explanations would be difficult to rule out.

In the examples below we consider cases where cultural factors come to be more involved in the development of a phenotypic trait, or less so. If culturally based transmission does indeed qualify as an inheritance system, then these are not just cases of change in developmental resources (§2), but also of transfer between inheritance systems proper. For example, if the initial evolution of dairy farming was partly due to selection of culturally transmitted factors, and these were underpinned by mechanisms that were designed to transmit phenotypes down the generations (as we have argued learning by overimitation might be), then the suite of practices forming the dairy farming phenotype was indeed transmitted by a cultural inheritance system. We know this generated selection pressures for genetic changes, such as lactose tolerance (Tishkoff et al. 2006). We can imagine one population undergoing sufficient genetic changes that a genetically-deficient individual in

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4 If there has been selection for mechanisms that stabilise membrane-based inheritance over and above stabilising the integrity of membranes in ontogeny, then it would qualify as a (limited) inheritance system.

5 Some inheritance systems may have been selected to have medium fidelity of transmission, with the function of transmitting phenotypes down multiple generations, but many fewer generations than are usually involved in genetic transmission.

6 That there is cultural *heritability* does not entail that there is a cultural inheritance *system*, on our more stringent account of the latter. A particular culturally copied phenotype can confer a fitness advantage on individuals or groups without culture being a system that is itself selected for transmitting adaptive variation down the generations.

that population would be unable to become a dairy farmer (e.g. because of allergies), in which case genetic inheritance would have become integrally involved in transmission of the dairy farming phenotype in that population. The phenotype remains homologous, however, with its wholly culturally transmitted ancestor and the latter's descendant cultural populations that have undergone no genetic changes in relation to lactose tolerance.

We envision two evolutionary developmental scenarios in which homology can be preserved across a change in inheritance system: one in which culturally transmitted phenotypes become environmentally canalized through a process of 'genetic assimilation' and thereby become partly genetically transmitted; and another in which genetic transmission comes to be superseded by cultural processes in accordance with what we will call 'cultural assimilation'. Our aim is to show that if the mechanisms of cultural evolution qualify as inheritance systems, then homology relations can survive across changes in transmission between genetic and cultural inheritance systems. This suggests that homology relations can survive even a *complete decoupling from the genetic inheritance system*—a possibility that, as we will see in §7, has often been overlooked in evolutionary psychology and anthropology. Though the scenarios we will discuss remain speculative and their relative frequencies unknown, genetic and cultural assimilation present two theoretically plausible avenues through which homology can cross inheritance systems. We discuss each of these in turn.

5.2 Genetic Assimilation

In the process of genetic assimilation (Waddington 1953), an initially plastic character is converted into a genetically heritable trait by selection acting on mutations that flatten the relevant reaction norm (Pigliucci, Murren and Schlichting 2007). Waddington offered the example of ostriches born with calluses at points where their skin will later abrade the ground, without their having experienced the friction that is the usual mechanism of callus formation. According to Waddington, the selection-based flattening and steepening of ubiquitous reaction norms is a fundamental feature of any causal interactionist picture of evolutionary development. This does not pose an obstacle to homology, since the flattening and steepening of the reaction norm alters how a trait is acquired ontogenetically, but it need not break the chain of phenotypic transmission itself.

There is no reason in principle why the general mechanism identified by Waddington could not involve the genetic assimilation of a culturally learned phenotype, which would become less dependent on cultural input for its development and more canalized against cultural variation. To argue that this might indeed happen in practice, we point to the possibility of a more specialised selection process identified by Papineau (2005). His model envisages a complex adaptive phenotype comprised of a series of subcomponents that are individually necessary and only jointly sufficient for production of the trait. For instance, making use of a particular foodstuff may require a multi-stage extraction and purification process. Assuming that none of the subcomponents confers a selective advantage on its own, it would be fantastically improbable for all the subcomponents to arise simultaneously as a result of genetic mutation/recombination. Papineau's idea is that, if the subcomponents are

learnable, then the complex trait might be accessible in phenotype space through learning, provided the benefits of the trait outweigh the considerable costs of acquiring all the necessary subcomponents through learning.

To keep things simple, Papineau proposes a model in which each subcomponent is under the control of a single genetic locus, with one allele genetically determining the sub-trait and an alternative allele rendering it plastic (and hence learnable). The plastic alleles make the complex trait accessible in the first instance, since arbitrary combinations of the subcomponents can be tried out much more quickly in developmental time than they can in phylogenetic time. Although still improbable, this could allow an individual to hit upon the complex phenotype entirely through learning. It is also plausible that, once discovered, the complex trait would be learnt by others and culturally transmitted. In a population where many individuals acquire all of the subcomponents through cultural learning, each non-plastic allele increases the probability of acquisition of one of the subcomponents, and hence of the complex trait. As a result, there will be selection pressure for the non-plastic allele at each locus, gradually leading to full genetic assimilation of the complex phenotype.

To turn this into a case of transfer between inheritance systems, we add to Papineau's model the plausible assumption that the initial cultural transmission of the subcomponents of the complex phenotype was achieved at least in part by mechanisms that qualify as an inheritance system. The result of the genetic assimilation identified by Papineau is that development stops depending on these culturally transmitted resources (i.e., it becomes canalized against such variations), with the genetic inheritance system becoming involved in transmission of the complex phenotype in their place. Although the phenotype shifts from being wholly culturally transmitted to being at least partly genetically transmitted, an unbroken chain of phenotypic similarity is maintained down the lineage, persisting across these changes in underlying developmental resources (Fig. 2). The descendant phenotype is therefore homologous with the similar phenotype in its ancestors. Furthermore, if the phenotype were found in two extant lineages, in one of which it had undergone less or even no genetic assimilation, then the trait would still be homologous as between the two lineages, despite differences in the inheritance systems involved.

[INSERT FIGURE 2 HERE]

Papineau's model is purely theoretical and we are unaware of any well-documented cases of genetic assimilation in the cultural context. Deacon (2003) plausibly suggests that language is a product of genetic assimilation, and if he is correct then there may at one time have existed two hominin lineages possessing a homologous linguistic adaptation, one of which was culturally transmitted (the ancestral developmental condition) and the other relying increasingly on genetic transmission (the derived developmental condition). Since very little is known about the genetics, cognition and behaviour of early hominins, it is simply too early to gauge the frequency or evolutionary significance of such events. It is important however, when theorising about human evolution, to be aware of the possibility that homologies might exist across such large differences in inheritance systems (see §6).

5.3 Cultural Assimilation

Now we consider whether a genetically transmitted trait such as a behavioural or cognitive adaptation could come to be culturally transmitted. This would be akin to a reverse Baldwin effect, whereby a trait that was previously transmitted by the genetic inheritance system comes to be acquired through learning in ontogeny. This scenario is different from the steepening of reaction norms contemplated by Waddington, because the phenotype need not become more generally plastic and may remain canalized against many forms of environmental variation, but with culturally transmitted resources coming to be responsible for more of the canalization.

To our knowledge there is no technical term in the literature to describe the evolutionary scenario whereby a genetically transmitted trait evolves to rely at least in part on cultural inheritance systems for its transmission. To distinguish this possibility from other forms of genetic accommodation we use the term 'cultural assimilation'.[7] We consider two scenarios in which cultural assimilation of a genetically transmitted phenotype might occur, the first due to cultural selection reacting more quickly to changes in selective regime, the second resulting from developmental drift under relaxed genetic selection due to culture-induced functional redundancy.

The first scenario for cultural assimilation relies on the fact that cultural selection can respond to changes in selective environments more rapidly than gene-based selection can. Consider a population in a heterogeneous selective environment in which distinct geographic patches are characterized by distinct stable selection pressures. Even when gene flow is not restricted, different phenotypes can and do evolve in different patches (Brandon 1990). In a cultural species, selective heterogeneity can result from different cultural practices or lifeways, which could produce a selection pressure toward the cultural assimilation of a previously genetically transmitted phenotype (Fig. 3).

[INSERT FIGURE 3 HERE]

The theoretical point can be illustrated with a stylised example, caricatured for the sake of clarity. Consider a population of hunter-gatherer hominins with a genetically transmitted tendency to kill large, vulnerable animals whenever they are encountered. Now suppose that over evolutionary time a cultural group emerges that adopts a farming lifestyle that includes dependence on domesticated animals. The optimal behaviour in relation to certain large vulnerable animals is now different, entailing that individuals protect rather than kill vulnerable domesticates. Let us stipulate that the 'protect' behaviour is not readily

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[7] 'Cultural assimilation' in the sense used here is to be distinguished from the scenario wherein a trait not transmitted by *any* inheritance system (e.g., an individually learned trait) comes to be culturally transmitted. The process just described, which is arguably common in cultural evolution (Gers 2011), is a cultural analog of genetic assimilation, but not one that would involve the shift across inheritance systems that we contemplate in this paper. Note that if one takes a broader view of cultural assimilation such that it includes the cultural cooptation and transmission of individually learned behaviors, then the process of cultural assimilation need not begin with a genetic mutation or innovation.

accessible through genetic mutation whereas the 'kill' phenotype is. Instead, the 'protect' behaviour is accessible through a mutation for behavioural plasticity, combined with cultural learning of the ecologically appropriate treatment of domesticates. Given significant gene flow between cultural groups, the hunter-gatherer lineage would also become plastic in their animal-response behaviour, but with little selective cost because the pre-existing 'kill' phenotype is already present and readily available for cultural acquisition. The effect of selection for cultural transmission of the 'protect' phenotype in the farmers is to make the 'kill' phenotype culturally transmitted in the hunters. There would then be no break in the 'kill' trait in the hunter-gatherers, preserving homology relations across inheritance systems.

In the second scenario, a genetic function is rendered selectively redundant due to the reliable cultural acquisition of the relevant trait, which is culturally copied in a population from its initial genetic origin. It is well established in molecular evolutionary biology that gene duplication can result in functional redundancy that relaxes stabilising selection and allows one of the duplicates to vary without negatively impacting on fitness (Lynch and Conery 2000; Wagner 2008). Much as gene duplications are subject to mutation and random drift in the absence of selection, so too are genetic variants that have become functionally redundant due to cultural transmission of their associated phenotype. If all genetic variants initially selected for producing the trait have degraded in this manner, or gone extinct, then the process of cultural assimilation would be complete.

Cultural assimilation would not occur if it were significantly more costly to acquire the trait through cultural learning rather than automatically via genetic resources (an assumption made by Papineau's model in §5.2 above). However, it is plausible that the costs might be symmetrical in some cases, since high-fidelity cultural transmission processes like 'blind' copying by overimitation do not incur the costs of individual trial and error learning. Indeed, cultural assimilation may occur as a more or less automatic result of general mechanisms of cultural learning, once genetic selection has raised the populational frequency of the trait to a significant level. In this way, cultural transmission could take off before gene-based selection has driven the trait to fixation, reducing selection pressures on the genetic variant and increasing the chance that it will be subject to stochastic extinction (Fig. 4).

[INSERT FIGURE 4 HERE]

Cultural assimilation may be further driven by its ability to break down pleiotropic linkages that constrain genetic evolution. Pleiotropy refers to the situation in which a gene associated with a fitness-enhancing trait has non-selected (and often deleterious) effects on other traits. If these deleterious collateral consequences are severe, even a highly fitness enhancing trait could be purged from the gene pool. By decoupling a trait from its genetic origin, cultural assimilation could avoid these deleterious side effects, thus enabling a lineage to occupy fitness enhancing regions of adaptive space that pleiotropic effects would otherwise have placed off limits.

In both examples of cultural assimilation, a trait originates only once in an ancestral clade via genetic mutation or recombination, and is maintained continuously in a descendant lineage through mechanisms of social learning. The character state resemblance between the

ancestral and derived developmental conditions is a clear-cut case of homology, so long as it was exhibited by all historical populations dating back to their last common ancestor.

Although the two-way evolutionary interaction between genetic and cultural transmission has been rigorously investigated, the particular gene-culture interaction that we contemplate in the case of cultural assimilation has not to our knowledge been discussed or modeled in the literature on 'dual-inheritance'. Dual inheritance models have typically captured the causal evolutionary interaction between different traits underwritten by different modes of transmission. For instance, the cultural transmission of dairy farming created selection pressures for genes associated with lactose processing. Most examples of gene-culture coevolution are of this structure (e.g., yam cultivation generates selection for gene-based malaria resistance; culturally transmitted mate preference for trait T generates a genetic selection pressure for genes associated with T, etc.). The reverse causal sequence would see a genetic innovation (such as a gene for incest avoidance) generate a selection pressure for a cultural innovation (such as an incest taboo that reinforces the genetic trait).

In contrast, in cultural assimilation the presence of one trait does not generate a selection pressure for another. Rather, the whole system is under stabilizing selection for a single trait, the transmission of which is 'offloaded' from genes to social transmission. There are some gene-culture coevolutionary models that come closer to capturing these dynamics. For example, Laland (2008) offers a model showing that a genetic predisposition (e.g., right handedness) can be reinforced by cultural copying biases, which act in conjunction with genetic selection to drive the trait to some non-trivial frequency. Our account differs from such 'cultural reinforcement' models in that (1) it contemplates the complete extinction of the genetic basis due to sampling error, given the rapidity of cultural acquisition and its dampening effect on the relative fitness value of gene-based behavioral innovations, and (2) it considers the role of plasticity in a heterogeneous selective environment and how this might drive cultural assimilation processes.

In concluding this section, we note that homology relations will not be preserved in all instances where a selective function is transferred from genes to culture. Consider the universal human cultural adaptation for cooking, which functions as an external mode of digestion and a method for sanitizing potentially contaminated foods. Thermal processing increases the digestibility of nutrients per unit of food consumed, and it tenderizes high-collagen meats that would otherwise require substantial chewing expenditures (Carmody and Wrangham 2009). Cooking appears to have rendered a number of genetic functions otiose, including those associated with olfactory acuity and masticatory muscle strength (Powell 2012). While chewing meat and cooking meat perform the same *function*, in this case there is no *character resemblance* that calls for a homology assessment. Taxic homologies do not describe similar functions whatever their morphology, but rather similar morphologies whatever their function.

6. Extension to Alternative Homology Concepts

Thus far we have been working with the standard taxic homology concept. Does our point about homology crossing inheritance systems also apply to alternative, non-taxic accounts of homology?

The main idea behind the developmental account is that homology relations are grounded in shared mechanisms of development, rather than patterns of phenotypic similarity. Wagner (1989/2007) articulates this in terms of shared developmental constraints or genetic regulatory networks. Our central claim is that an unbroken lineage of phenotypic similarity can persist across large changes in developmental mechanisms, including across inheritance systems. Some prominent views of homology, such as Hall's (2008/2013) hierarchical account (see also Ramsey and Peterson 2012), have little conceptual difficulty accommodating such cases since they allow homology at one level to be decoupled from homology at a lower level. Such cases also fall un-problematically within the general taxic conception of homology that we have relied upon. In contrast, the cases of radical decoupling that we envision would not count as homologous on Wagner's account, despite the fact that they involve shared character states inherited continuously from a common ancestor and so count as homologous on the taxic conception. Given that Wagner focuses on shared "developmental constraints…caused by locally acting self-regulatory mechanisms of organ differentiation" (Wagner 1989, p. 62), it is not clear that his definition would apply to cognitive or behavioural phenotypes at all.

This is not all that surprising, given that the homology literature has tended to focus on structural morphology, rather than on behavior or aspects of the extended phenotype that may be the subject of cultural inheritance. There are strong reasons, however, to prefer a unified, hierarchical account of homology (e.g. Currie forthcoming) that can accommodate all aspects of the organism that are subject to phylogenetic assessment. Methodologically, the task of reconstructing evolutionary histories can be enriched and our phylogenetic hypotheses sharpened by incorporating behaviors and other non-structural traits into the analysis. Theoretically, a concept as fundamental as homology should be capable of unifying traits at all levels of the biological hierarchy—especially those that play important roles in ecology and evolution, as behavioral and cultural traits often do. Hierarchical accounts of homology have these methodological and unifying virtues. They can accommodate not only homologous non-structural phenotypes that have become decoupled from their structural, cognitive, or genetic moorings (Hall 2013), but also those that have undergone complete dissociation from their underlying developmental constraints—such as homologous traits that have undergone complete shifts across inheritance systems.

An alternative version of the developmental homology concept hinges on the same biological *information* being involved in the development of a trait over evolutionary time (Van Valen 1982; Roth 1991; Wiley and Lieberman 2011, 120-121). The lacuna in this view is to specify information in such a way that the same information sometimes is, and sometimes is not, involved in the development of similar traits. One version of this view (not necessarily attributable to the aforementioned authors) holds that the genome carries information which programs or specifies a given outcome, and that this biological

information can persist across changes in the patchwork of intervening developmental processes. We resist this account since, as discussed in §3, we doubt that genes program or specify phenotypic outcomes in anything like this sense. However, if informational resources could be adequately specified at the epigenetic or cultural level, there is no reason to think they could not survive the switch between genetic and cultural inheritance that we have contemplated in this paper, since information is not tied to any particular biological substrate. So again homology could subsist across a change in inheritance system.

In sum, although certain developmental homology accounts might be compatible with some of the homologies across inheritance systems that we identified above, these accounts either lack specificity or fail to cover cases where character similarities are clearly the result of common descent and should thus be counted as homologies.

7. Illustration: The Phylogeny of Intergroup Violence in Hominins

We will now consider the implications of the above discussion for debates over the phylogeny of similar behaviours in humans and chimpanzees. For illustrative purposes, we will focus on one widely discussed trait resemblance: male-initiated intergroup aggression. Does human out-group violence originate in our common ancestry with chimps?

Some sociocultural anthropologists have rejected the notion that we have much to learn about the origins of complex cognitive and behavioural traits in humans by studying their ostensible precursors in chimpanzees and other primates (Marks 2003). This conclusion is partly based on observations indicating that many behavioural characteristics that humans appear to share with chimpanzees, such as intergroup violence, infanticide and patriarchal social relations, are culturally sensitive in humans but not in chimps (Sponsel 2010; Sussman 1999; Bock 1980). The coupling of homology judgments to developmental properties is evident in the Seville Statement of 1986 on the biology of human aggression, adopted by UNESCO and endorsed by more than a dozen scientific and professional associations (Adams and Buchanan 1990):

> [I]t is scientifically incorrect to say that we have inherited a tendency to make war from our animal ancestors…The fact that warfare has changed so radically over time indicates that it is a product of culture (First Proposition).

Fundamental differences in developmental acquisition are thus taken to imply that intergroup aggression in humans and chimps is not the result of shared ancestry.

Evolutionary psychologists who are inclined to consult the cognitive and behavioural characteristics of chimpanzees in order to gain insights into the origins of similar traits in the human lineage have done little to challenge this assumption. If anything, they have reinforced it by tying homology judgments to inferences and arguments about genetically evolved propensities, and by contrasting these with traits that develop under primarily cultural influences (e.g. Van Vugt 2009; Wrangham 2010/1995). For example, where a similar cognitive or behavioural trait that humans share with other primates (e.g., a 'sense of fairness') is acquired in humans via a general cultural learning device, evolutionary psychologists tend to conclude that the trait is non-homologous and perhaps not even an

evolved trait at all (see, e.g., Machery and Mallon 2011). As noted in §2, such authors appear to reason as follows: if a behavioural trait exhibited by humans and a closely related taxon is homologous, then it follows that the trait in both clades is genetically transmitted and resistant to cultural perturbation (*cf.* Ehrlich 2000, 210; Kitcher 1987, 64-65).

'Intergroup aggression' refers to one social group cooperating in threatening, chasing, striking, wounding or killing members of conspecific groups. This often involves 'raiding', in which bands of males from one social group 'hunt', ambush and kill members of another group. Pre-meditated, fatal attacks on neighbouring groups are routinely carried out by common chimpanzees (Wilson and Wrangham 2003), often involving horrific mutilation of the victim that goes well beyond sufficient lethal force. There are of course significant differences between human and chimp manifestations of intergroup violence – language-based coordination and the use of technical weaponry are dimensions of warfare that are obviously lacking in chimps. But homology relations rest not on identity but similarity. Cultural traits like intergroup violence may vary in structure and function, much as the forelimbs of bats and giraffes vary in structure and function, but they will still be homologous so long as the similarities they do exhibit are the result of continuous descent from a common ancestor.

In their seminal paper comparing adaptive intergroup violence in chimpanzees and human hunter-gatherer groups, Manson and Wrangham (1991, 370) wrote that "[t]he similarities between chimpanzees and humans suggest a common evolutionary background. Thus, they indicate that lethal male raiding could have had precultural origins and might be elicited by the same set of conditions among humans as among chimpanzees." One might read this passage as implying that intergroup violence is homologous, having evolved only once in a common ancestor of humans and chimps. In their reply to commentaries, however, Manson and Wrangham (1991, 385) made it clear that by 'common evolutionary background', they meant only to suggest that intergroup violence might have evolved under similar ecological conditions in both lineages.

Subsequently, however, Wrangham (1995) argued for homology on the grounds that coalitional violence appears to be genetically transmitted and developmentally canalized in both lineages. Because humans and chimps seem to share these 'innate' behavioural dispositions and psychological mechanisms:

> The implication is that strong aspects of human violence have long evolutionary roots…In our aggressive urges we are not Gauguin's creatures of culture. We are apes of nature cursed over 6 million years or more with a rare inheritance, a Dostoyevskyan demon…The coincidence of demonic aggression in ourselves and our closest kin bespeaks its antiquity (1995, 7).

Likewise, in *Demonic Males* (1996), Wrangham and Peterson suggest that coalitional violence is genetically based in both lineages and may be traced continuously all the way back to the last common ancestor. Although Wrangham (2010) concedes that this phylogenetic question remains unresolved, he assumes that its resolution will turn on genetic or neurobiological data, thereby coupling the mode of ontogeny with evidence for or against continuous phylogeny. Thus, Wrangham and colleagues tie homology judgments to shared

developmental profile, and implicitly endorse the reverse: that is, an inference from disparate developmental profile to non-homology. Many anthropologists rely on the same conditional but reach the opposite conclusion, because they think that intergroup violence in humans is culturally acquired rather than genetically specified (see e.g. Bock 1980, 76), and thus they reject the claim that we are observing the same (read: continuously transmitted) character in chimps and humans (Sussman 1999).

While we have acknowledged that the developmental basis of a character resemblance is relevant to assessing homology, we have also argued that it is not definitive. Even if the tendency to direct aggression toward out-group members is culturally sensitive in humans but culturally insensitive in chimpanzees, this alone does not entail that the traits are non-homologous. We do not dispute the general applicability of the principle of "evolutionary parsimony" (de Waal 1997), which holds that a shared trait in closely related taxa is likely produced by shared proximate mechanisms. But this principle should be applied cautiously in the case of labile behavioral traits, and even more carefully in the context of robustly cultural species. The phylogeny of intergroup violence is unclear on the present state of the evidence, and is complicated by the relatively peaceful bonobo, which is as closely related to humans as is the common chimpanzee. Our aim here is not to review the evidence. We only wish to argue that homology in relation to any trait, be it cognitive, behavioral or morphological, should not hang on shared developmental mechanisms or shared inheritance systems, as has often been assumed. This is particularly true in the case of species that rely heavily on social learning for their development, since homologies can subsist across shifts between genetic and cultural inheritance systems.

We have focused on the conceptual question as to whether homology can be preserved across inheritance systems, and we have investigated the theoretical plausibility of this result. We have said little about the epistemic difficulties that are likely to be encountered in attempting to identify actual instances of this phenomenon. It seems to us, however, that these epistemic challenges are comparable in kind and magnitude to those confronting homology/homoplasy assessments of character resemblances with disparate developmental underpinnings in general, and of behavioral resemblances in particular—and we believe that the methods employed to address these challenges in the present case would be correspondingly similar (*cf.* Rendall and Di Fiore 2007, 518).

Even if it could be determined with high levels of confidence that, for example, the last common ancestor of chimps and humans exhibited intergroup aggression, how could we be reasonably certain that this trait was *continuously* transmitted in *Pan* and *Homo* lines since their split, only to be lost in the bonobo? The epistemic problem of inferring continuous transmission of a putative ancestral trait is one that confronts phylogenetic reconstruction in general, and need not pose any particular difficulties for the phylogenetic reconstruction of behavioral traits. Nevertheless, complications arise in relation to plastic or dispositional traits—to wit, traits that are conditionally expressed or that develop only in certain environments (as is the case for many behaviors, such as the dominance displays of high-ranking males). This has led some homology theorists, such as Ramsey and Peterson (2012), to hold that homology can be preserved despite a break in phenotypic continuity so long as

there is continuity "one level down" in development (such as a continuously transmitted genetic disposition for a plastic trait). We maintain, however, following Currie (forthcoming), that a dispositional account of characters is sufficient to establish phenotypic continuity in cases of conditionally expressed traits. On this view, phenotypic continuity can be established via analysis of developmental counterfactuals: If it can be shown that non-pathological ancestral individuals or populations would have expressed descendent trait T (e.g. intergroup violence) had such and such environmental conditions been present, then phenotypic continuity in T will have been established.[8]

8. Conclusion

Culture is not a mere byproduct of the collective human imagination or capacity for rational agency. It is very likely to be, at least in some crucial respects, an adaptive product of biological evolution. If it is more than that, and aspects of cultural transmission have been designed for the ability to transmit phenotypic variants down the generations, then there are one or more cultural inheritance systems. And as we have shown, homology relations can be preserved across changes between genetic and cultural streams of inheritance. The frequency and evolutionary significance of phenomena like genetic and cultural assimilation remain unknown. In any case, it is an important feature of the homology concept that it can transcend the developmental constraints and even inheritance systems underlying a character resemblance. Wrangham (1995, 7) may be correct that 'the coincidence of demonic aggression in ourselves and our closest kin bespeaks its antiquity', but we should not assume that the antiquity of a trait implies that it must be produced by the same developmental mechanisms, or transmitted by the same inheritance system, in modern humans.

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8 Further complications arise due to the fact that selection on conserved developmental mechanisms can result in the repeated origination (and loss) of a trait in a bushy clade (i.e., 'parallelism')—which one may (Ramsey and Peterson 2012) or may not (Currie forthcoming) prefer to categorize as homologs. Furthermore, one might think that behavioural traits, such as intergroup hostility, will be especially prone to iterated evolution, given that they are labile, only loosely tied to structure, and partly functionally delineated. In fact, insofar as this lability entails greater degrees of freedom in alternative character state space, the phylogenetic signal of behaviors and culturally acquired traits will be less prone to homoplastic noise (Rendall and Di Fiore 2007). In any case, these are epistemic difficulties that confront the homologization of behavioral characters in general, not simply those implicating cultural traits or shifts across inheritance systems. A full treatment of these important issues lies beyond the scope of the present discussion.

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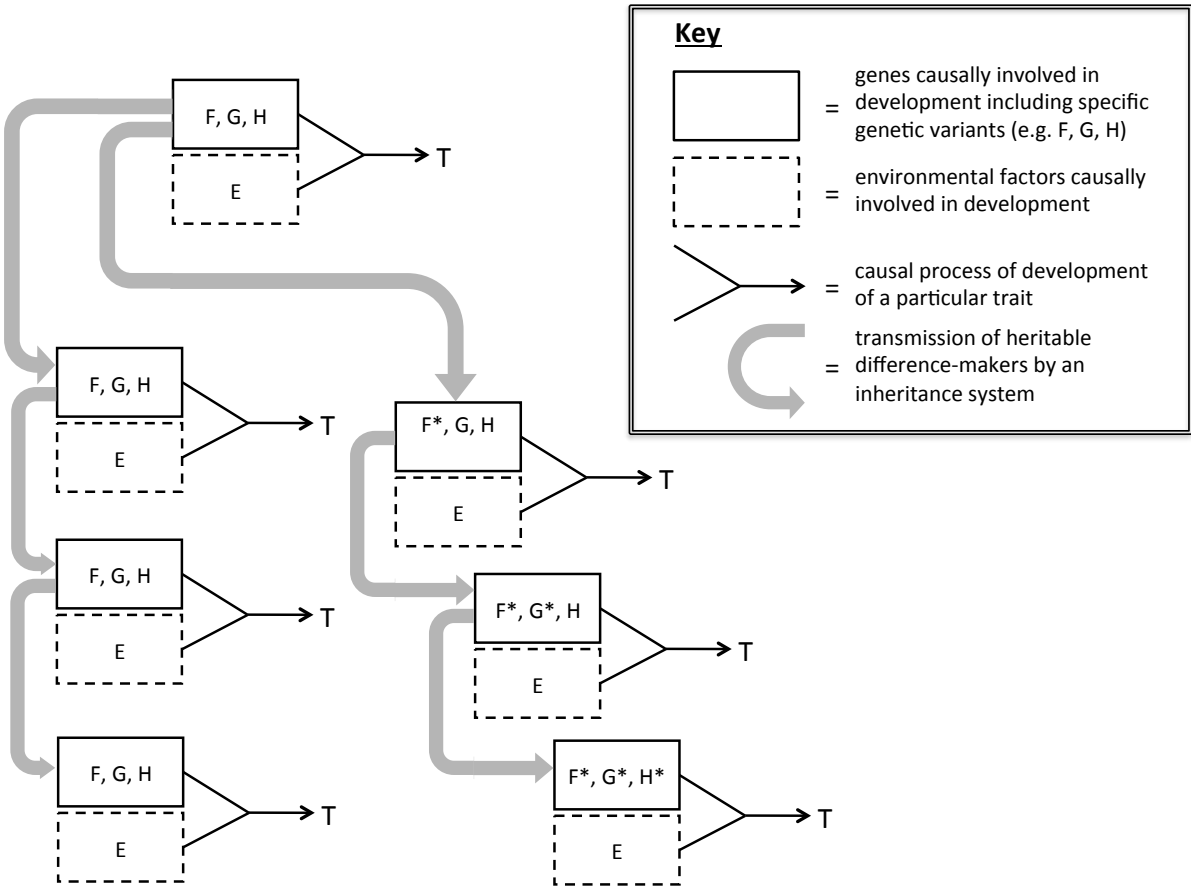
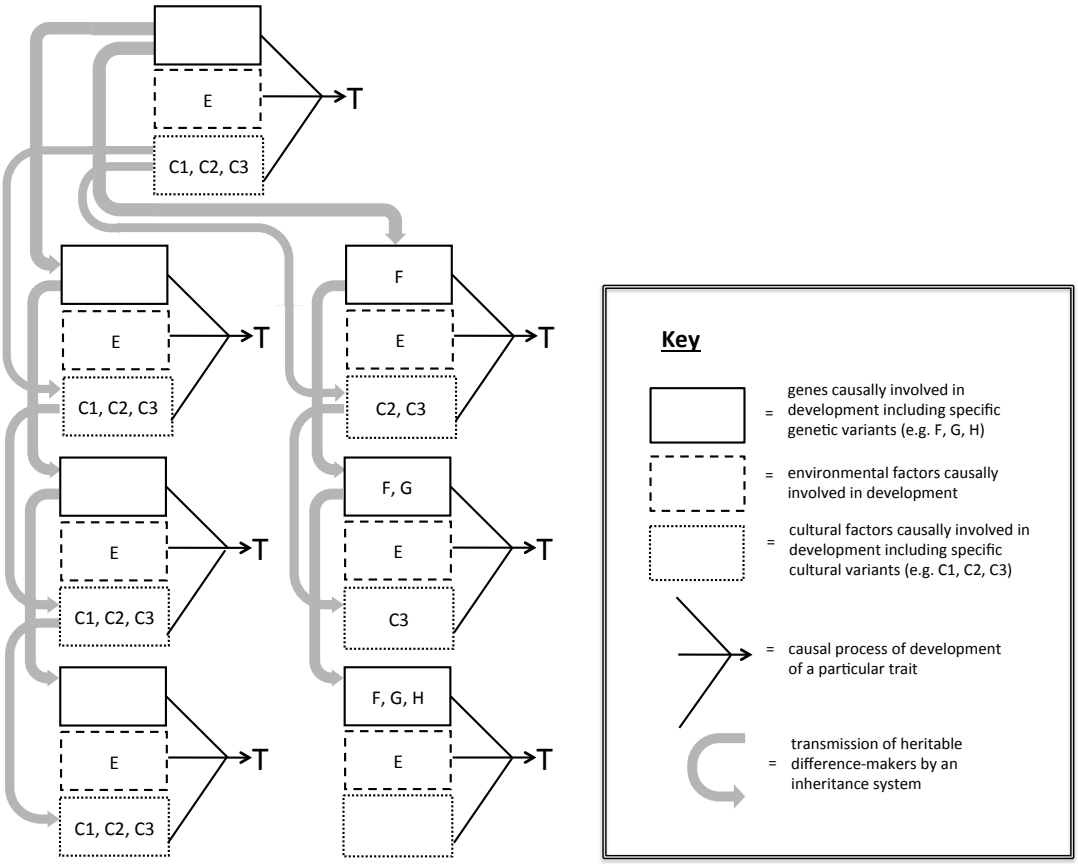
FIGURE 1. Homology Across Genetic Turnover



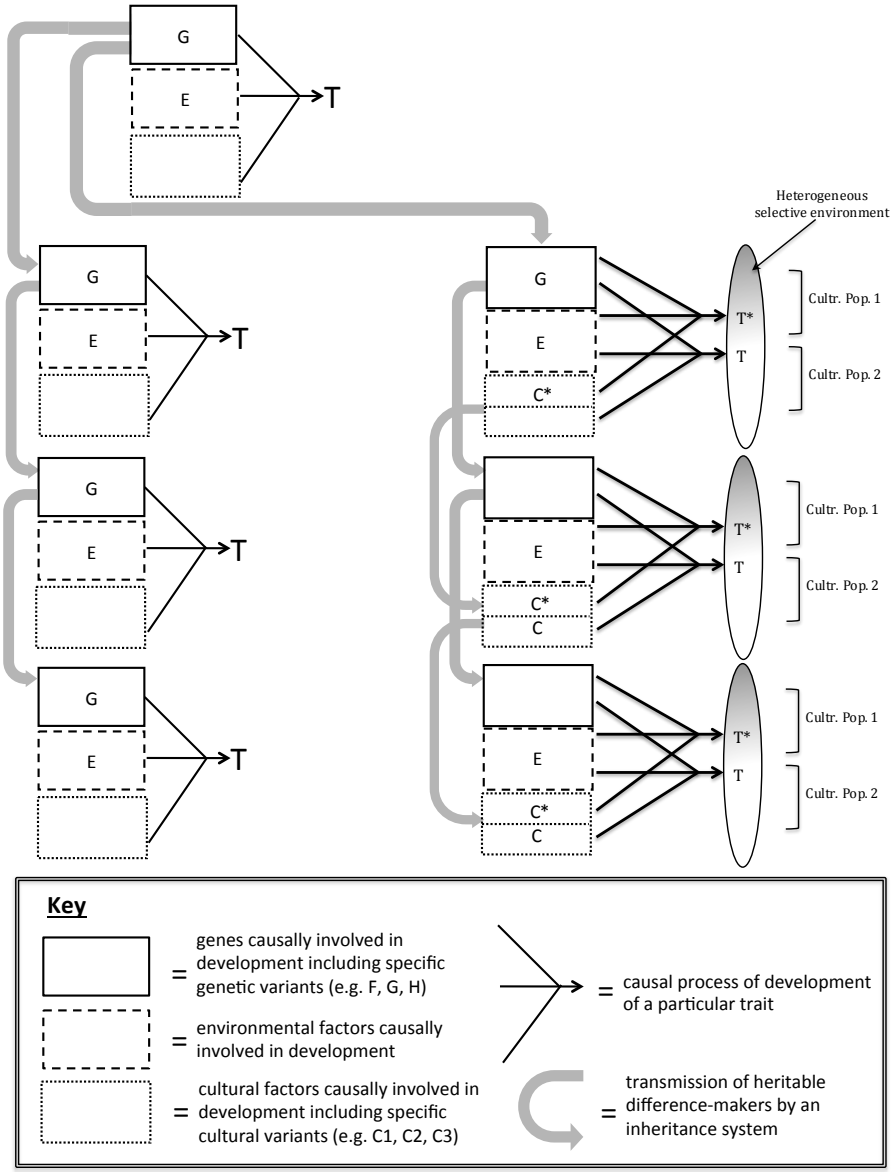
Ancestors are shown at the top of the diagram. In the right-hand lineage three of the genes ancestrally involved in development of trait T become replaced by alternative genetic causes, while in the left-hand lineage the ancestral developmental condition is retained. Trait T remains homologous between the two lineages at the end of the process.

FIGURE 2. Genetic Assimilation



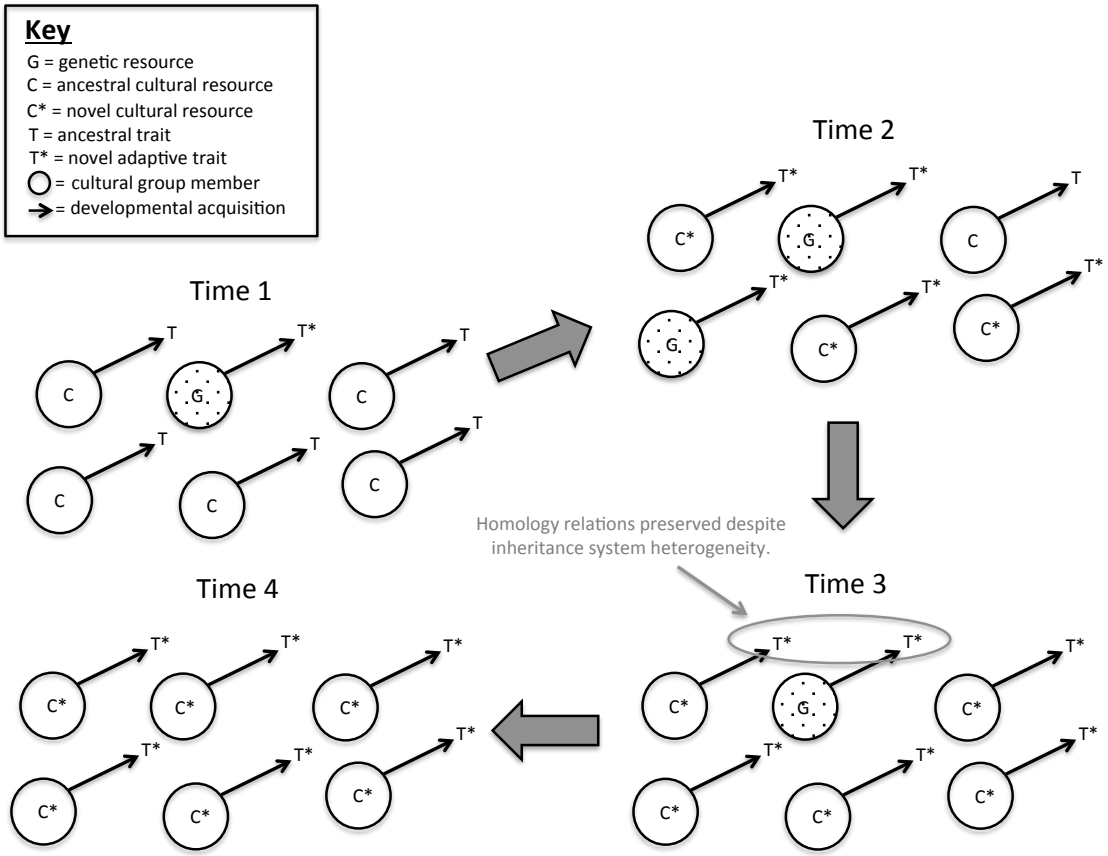
In the right-hand lineage, culturally transmitted resources ancestrally involved in the development of trait T become progressively replaced by genes (which bias development towards T), while in the left-hand lineage the ancestral developmental condition is retained. T remains homologous between the two lineages at the end of the process.

FIGURE 3. Cultural Assimilation: Case 1



In the right-hand lineage, which occupies a stable heterogeneous selective environment with respect to ancestral trait T, a new culturally transmitted practice C* gives rise to novel adaptive trait T* in cultural population 1, while in cultural population 2 T remains adaptive and gene G, along with a non-cultural environment, ensures the reliable development of T. That introduces a selection pressure against G (which biases development towards T) in population 1, causing a new cultural variant C to become causally involved in the development of T in population 2. As a result, transmission of C by a cultural inheritance system becomes crucial for the maintenance of what was previously a gene-based trait within that cultural group. At the end of the process, T remains homologous between the left-hand lineage and those individuals in the right-hand lineage who exhibit T.

FIGURE 4. Cultural Assimilation: Case 2



At Time 1 in a cultural population, novel genetic variant G increases the probability of acquiring adaptive behavioural trait T*, which is a fitness-enhancing modification of cultural ancestral trait T. At Time 2, G (and hence T*) increases in frequency in the population, while group members lacking G begin to develop T* through social learning from extant examples of T* using novel cultural resource C* to acquire the successful strategy. Cultural acquisition of T* nullifies the relative fitness advantage of G and, given G's low standing frequency in the population, sets the stage for its stochastic extinction as shown at Times 3 and 4, resulting in full cultural assimilation of T*. Note that although at Time 3 the population remains heterogeneous with respect to the inheritance system transmitting T*, all instances of T* are homologous since they descend from a common populational ancestor which possessed T*.