GENE-CULTURE COEVOLUTION:
A BROADER EVOLUTIONARY PERSPECTIVE

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Abstract

Gene-culture coevolution (GCC) stands out among approaches to human evolution for its ambitious synthesis of biological and social sciences. Combining insights from cultural evolution and human genetics, it has been invoked to explain the evolution of many "species-defining" human traits, from language to large-scale cooperation. However, despite its broad conceptual appeal, empirical evidence for GCC is often perceived as limited to a few "classic" examples, such as lactase persistence. We propose that this apparent gap between theoretical significance and empirical support may partly derive from conceptual ambiguities about what kind of gene-culture interactions truly constitute gene-culture coevolution. Drawing on recent work on gene-culture coevolution in animals and examples from the human genomics literature, we argue that a broader conception of gene-culture coevolution, explicitly incorporating drift and migration, provides a more comprehensive understanding of human evolutionary dynamics. Our approach, which we term "broad gene-culture coevolution," builds upon and

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subsumes the existing “narrow” framework that primarily emphasises selective processes. We illustrate the utility of this expanded perspective through two case studies: the evolution of skin pigmentation and the influence of trade networks on genetic variation in Melanesia. By integrating insights from anthropology, genetics, and cultural evolution, we demonstrate how cultural factors can shape both adaptive and neutral genetic variation and population structure. This broader framework not only accommodates a wider range of empirical findings but also opens new avenues for hypothesis generation and testing in the study of human biocultural evolution. We conclude by discussing the boundaries of this approach and its potential to synthesise diverse disciplinary perspectives, ultimately providing a more nuanced understanding of how humans have shaped their own evolution.

***K*eywords** Gene-culture coevolution · Cultural evolution · Niche construction · Human genomics · Local adaptation · Neutral evolution · Migration · Lactase persistence

1 Introduction

A new perspective on human evolution has emerged over the past fifty years that attempts to reconcile insights from both the “natural” and “social” sciences into a single comprehensive formal framework, with the aim to explain the perhaps unusual evolutionary trajectory of the human species. Variously labelled as ‘gene-culture coevolution’ (Feldman and Laland 1996, used exclusively hereafter), ‘culture-gene coevolution’ (Chudek and Henrich 2011) or ‘dual inheritance theory’ (Boyd and Richerson 1985), this approach posits that genes and culture represent two separate, yet deeply intertwined, inheritance mechanisms which may result in (potentially adaptive, but occasionally maladaptive) phenotypic change over time (Durham 1991; Cavalli-Sforza and Feldman 1973, 1981; Aoki 2001; Richerson, Boyd, and Henrich 2010; Richerson and Boyd 2005). The fact that “species-defining” human phenotypes - for example our capacity for language, technology, cooperation and complex problem solving - are not solely determined by genetic variation, but subject to a rich causal mosaic of interacting factors, including the cultural environment, is almost universally uncontroversial (McGue and Bouchard 1998; Nisbett et al. 2012; Uchiyama, Spicer, and Muthukrishna 2021). Naturally, the study of such interactions is not the exclusive purview of gene-culture coevolutionary theory, as it is, for example, also features in the study of gene-environment interactions (see Hunter 2005; Manuck and McCaffery 2014). However, the evolutionary significance of this interplay is likely best elucidated through a theoretically rigorous and empirically grounded science of gene-culture coevolution.

Clearly, such a broad and ambitious scientific endeavour requires conceptual clarity - a clarity, we argue, that at times perhaps escapes this maturing field of study. In the present paper, we set out to rectify this by interrogating and subsequently expanding what researchers traditionally mean by “gene-culture coevolution”. We first query the central scientific motivations behind applying gene-culture coevolutionary frameworks. We then outline *narrow gene-culture coevolution*, which we characterise as the more traditional and commonly applied approach, before subsequently introducing and illustrating an expansion upon that framework which we call *broad gene-culture coevolution.* This broader framework calls for the inclusion of non-selective mechanisms, namely drift and migration, into gene-culture coevolutionary thought and theory, the productivity of which we aim to illustrate by presenting two examples of the way culture interacts with these processes: The buffering role of cultural traits in the adaptive evolution of skin pigmentation, and the way that migration by ways of a traditional trading network, the *Kula* ring, may have shaped genetic patterns in Oceania. We finish by considering the limitations and boundaries of this expanded approach, and briefly outlining a way forward for the wider field.

1.1 Core concepts and research aims in the study of gene-culture coevolution

The central ideas of gene-culture coevolution have changed relatively little since its inception through the pioneering work of Feldman and Cavalli-Sforza (Cavalli-Sforza and Feldman 1981), and later Boyd and Richerson (Boyd and Richerson 1985). At its core, it shares with broader cultural evolutionary theory a commitment to the assumption that the population-level transmission dynamics of cultural information mimic biological evolution sufficiently to allow for an evolutionary framework of cultural change (Mesoudi 2011). However, it extends beyond this through another central concept: The dependence, and sometimes co-dependence, of genotype and cultural phenotype. For example, the term "gene-culture coevolution" is often applied to instances where, by modifying ecological conditions, cultural traits shape the form of natural selection acting on the population's genome. Another definition of (gene-culture) coevolution is more closely aligned with the use of the term 'coevolution' invoked in ecology and evolution (Janzen 1980). Specifically, this more demanding definition relates to a deeper and bi-directional causal interdependence between the coevolving elements - or, more precisely, *dynamic reciprocal evolutionary change* - most often in the form of *specific coadaptation* marked by reciprocal influences on the relative fitness of interacting traits and specific phenotypes (Thompson 1989). Accordingly, a key aspect of gene-culture coevolution theory is that the biological and cultural evolutionary processes interact through continuous causal feedback loops: Genetic propensities or otherwise biologically rooted predisposition towards certain relevant phenotypes (e.g. evolved perceptual, motivational or cognitive biases) may shape what and how cultural information is acquired, stored and transmitted, while at the same time, cultural practices can modify the ecological conditions that are the source of natural selection affecting the human genome, including genotypes underlying the traits which enable and amplify enculturation in the first place (Laland 2017; J. R. Kendal 2015).

Strikingly, many definitions of gene-culture coevolution mirror, explicitly or implicitly, the coevolution-through-coadaptation conception that dominates evolutionary ecology. Their proponents, among them many of the field's key contributors, appear primarily concerned with gene-culture interactions that lead to "new selective pressures" (Richerson, Boyd, and Henrich 2010, 8985), to "selection [. . .] generated or modified by [culture]" (Feldman and Laland 1996, 453), or that become the "basis for genetic selection" (Gintis 2011, 879). In other words, the focus clearly appears to be on *selective* processes - and especially on cases where cultural elements modify the natural selection of genetic variation, but where, in practice, the requirement to demonstrate reciprocal adaptation often appears to have been relaxed. This may be partially accounted for by the fact that gene-culture coevolution often appears to be invoked primarily as a framework to explain *form and function* of evolved cultural and biological traits, as well as their perceived distinctiveness. In this context, an overtly selection-focused (hereafter: *narrow gene-culture coevolution*) approach can certainly be productive. Gene-culture coevolutionary approaches intent on explaining distinct phenotypes, for example large-scale cooperation or musicality, employ gene-culture coevolutionary theory in this fashion (Gintis 2011; Chudek and Henrich 2011; Savage et al. 2021).

Our key contention is that if, conversely, the aim of gene-culture coevolutionary research is to elucidate the wider evolutionary dynamics of species with a rich cultural capability, humans chiefly among them, then a wider repertoire of gene-culture interactive processes need to be considered to fully account for the emergence of and change in genetic and cultural variation. Indeed, this idea is reflected in more recent gene-culture coevolutionary work in nonhuman animals, such as whales, which has favoured a broad conception that recognizes the influence of culture on both adaptive *and* neutral (i.e. non-selective) evolutionary processes(Whitehead et al. 2019). As we describe below, genetic analyses suggest that human biological evolution since the emergence of our species is profoundly shaped, if not dominated, by drift, founder effects and gene flow, rather than natural selection (Ramachandran et al. 2005; Williamson et al. 2007; Simon and Coop 2024). This implies that a focus on selection alone is unlikely to uncover the full picture; other evolutionary processes, including (cultural impacts on) mutation, drift, and gene flow, also require investigation. In fact, it seems highly plausible that the current narrow focus of gene-culture coevolution by selection may inadvertently exclude some of the most interesting and significant forms of evolutionary interaction between genes and culture in our species. It is worth noting here that this approach does not reject what we have termed "narrow gene-culture coevolution", but rather subsumes it: a *broad* approach to gene-culture coevolution does not ignore selection, nor is it uninterested in adaptation - it merely places these phenomena in their wider evolutionary context. In short, we believe that definitions of gene-culture coevolution may differ in *scope* because the application of the framework may differ in *purpose.* This insight forms the basis for our conceptual rearrangement. In the subsequent sections, we aim to illustrate what we view to be the differences and boundaries of these narrow and broad conceptualisations of gene-culture coevolution. We propose that these differences in scope introduced above can be understood as a set of concentric or overlapping frameworks, with every additional layer extending and subsuming the previous ones (see Figures 1 and 2).

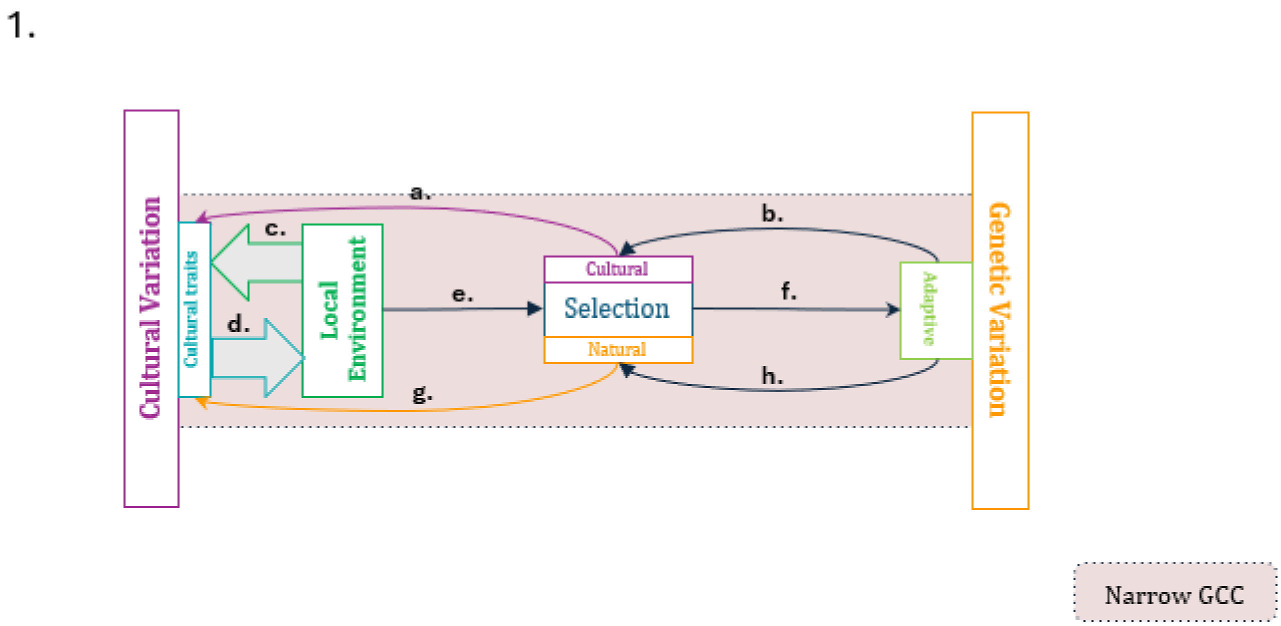

Figure 1: **Illustrative causal diagram for narrow gene-culture coevolution.** The arrows here represent the following causal interactions: a.) cultural selection on cultural variation, b.) genetically evolved (cognitive) biases in social learning, c.) population-level cultural adaptation (through individual-level learning), d.) cultural niche construction, e.) the eco-cultural environment as a source of selection, f.) natural selection of (adaptive) genetic variation, g.) natural selection of cultural variation, h.) genetic and developmental biases in the natural selection of cultural variation (e.g. evolved anatomical morphology, lactase persistence genotypes, etc.).

2 Modes of gene-culture coevolution

2.1 Narrow gene-culture coevolution

Narrow gene-culture coevolution focuses on the reciprocal action of selective processes on both cultural and genetic variation (see Figure 1). For one, culturally evolved traits and the local ecology can interact to form the selective environment (which we take to include both tangible and intangible features of the environment, e.g. both physical geography and social norms). At least in principle, this interaction, like many processes within this framework, is inherently reciprocal. Some cultural traits are adaptive and shaped by the local ecology (Mathew and Perreault 2015), as widely assumed within human behavioural ecology (see Micheletti et al. 2023). At the same time, culturally evolved traits profoundly shape both the local ecology itself (e.g. choosing or modifying the landscape) and the impact of ecological variation (e.g. buffering against seasonality), a phenomenon known as 'niche construction' (Day, Laland, and Odling-Smee 2003; J. R. Kendal, Tehrani, and Odling-Smee 2011). While the dynamics of these interactions are important avenues of research in themselves, the gene-culture coevolutionary framework primarily concerns their outcome: The eco-cultural "landscape" that sets the stage for genetic selection, which feeds back onto relevant adaptive genetic variation. Take the flagship example of gene-culture coevolution, lactase persistence (i.e. the ability to digest lactose into adulthood; see Box 1): eco-cultural dynamics like dairying practices and availability of grazing land lead to presence or absence (or varying extent) of dairy pastoralism, which in turn determines the fitness advantage of lactase persistence-related alleles, whose spread in turn impact the incidence and utility of dairying.

More generally, the genetic variation favoured by culturally modified natural selection may feed back to shape the selection acting on cultural variation in at least two ways: On one hand, both cognitive biases for intrinsic characters of certain cultural traits (Sperber 1996; Stubbersfield 2022) or a broader evolved psychology biased towards cultural learning may evolve (Henrich 2015; Laland 2017; R. L. Kendal et al. 2018), thereby shaping the action of *cultural selection,* meaning the biased transmission and spread of certain cultural variants (Richerson and Boyd 2005). On the other hand, genetic traits may also influence the fitness, and hence *natural selection* of individuals holding certain cultural traits, or certain variants of a particular cultural trait. In the lactase persistence example, the presence or absence of lactase persistence seems to have modified the fitness advantage of practicing dairy pastoralism within individuals (Gerbault et al. 2011). Taken together with the culturally-shaped selection on genotypes, these two pathways make up the reciprocal feedback loop fundamental to much classic gene-culture coevolutionary thought (Figure 1).

Box 1. Cultural modification of selection pressures - Dairy pastoralism and lactase persistence

Unquestionably the most prominent example of narrow sense gene-culture coevolution is the evolution of human adult lactose tolerance and the associated ability to digest dairy. Most humans, like most mammals, lose the ability to digest lactose, a disaccharide sugar that forms the principal component of milk, as they mature (Scrimshaw and Murray 1988). However, some populations have retained this ability, termed *lactase persistence* for the corresponding lactose-processing enzyme, due to genetic polymorphisms in the lactase gene LCT and associated regulatory regions such as MCM6 (Swallow 2003; Lewinsky et al. 2005; Ingram et al. 2009). Strikingly, these populations also tend to have a strong cultural history of cattle farming and milk consumption, giving rise to the now-classic gene-culture coevolutionary hypothesis that dairy farming, as a cultural practices that provided a novel abundant source of milk in the diet, may predate this adaptation and have shifted selection pressures to favour lactase persistence (Simoons 1969; McCracken 1971; Feldman and Cavalli-Sforza 1989; Holden and Mace 1997; Gerbault et al. 2011). It also showcases the potentially transformative power of gene-culture coevolution, as selection on LCT is some of the strongest selection documented in the human genome to date (Voight et al. 2006). While this represents a textbook example of gene-culture coevolution (e.g. Durham 1991), even the much-recounted story of lactase persistence is not fully understood and important aspects (e.g. the strength, timing and mechanisms of selection) are continually revisited and updated as new ancient DNA evidence emerges (Ségurel and Bon 2017; Campbell and Ranciaro 2021), highlighting the complexity of gene-culture coevolutionary inference even in the narrow sense (see also Evershed et al. 2022).

What is remarkable about the lactase example is the wide attention and general acceptance it has received in the scientific community as a cross-disciplinary phenomenon (Tishkoff et al. 2007), spanning genomics, medicine, anthropology, and archaeology, and compromising many hundreds published articles. This prominence has played a key role in the narrative that narrow gene-culture coevolution is not just a hypothetical possibility, leading geneticists and interdisciplinary teams to propose other candidate cases of gene-culture coevolution (albeit only rarely in the terms of that theory). For example, among indigenous Inuit populations of Greenland, there is evidence for extensive genetic adaptation to diets with a high content of polyunsaturated fats (or PUFAs), an adaptation that has been posited to be a direct function of the predominantly fishing-based subsistence of these Arctic marine hunters (Fumagalli et al. 2015; Deutch et al. 2007). Elsewhere, human dietary adaptations have been proposed for regulating the intake of a number of other macro- and micro-nutrients, including starch (Perry et al. 2007), iron (Heath et al. 2016), calcium (Hughes et al. 2008), zinc (Zhang et al. 2015), and selenium (White et al. 2015) - the relative abundance of each of which in human diets is often directly dependent on cultural influences on subsistence (Ulijaszek 2018). Local adaptation may also have shaped physiological responses to dietary by-products and toxins: Genes coding for alcohol dehydrogenase (ADH), an enzyme involved in the detoxification and processing of alcohol, exhibit remarkable geographic variation and signatures of recent selection (Osier et al. 2002; Han et al. 2007), leading some researchers to speculate that variants may represent a protective genetic response to cultural practices which gave rise to increased alcohol consumption, such as rice cultivation in East Asia (Peng et al. 2010).

Yet none of these studies match the lactase persistence case for the depth in which the coevolutionary dynamic of the underlying gene-culture interactions has been studied empirically, and hence they retain the status of plausible candidates rather than well-understood examples. Currently, many proposed gene-culture associations tend to be *ex post* explanations for inferred patterns of selection, or at best the result of temporally flat correlative studies between genetic and cultural traits, leaving much room for even this conceptualisation of gene-culture coevolution to be understood more deeply. In this context, lactase persistence deserves continued attention as a model case for cross-disciplinary inquiry.

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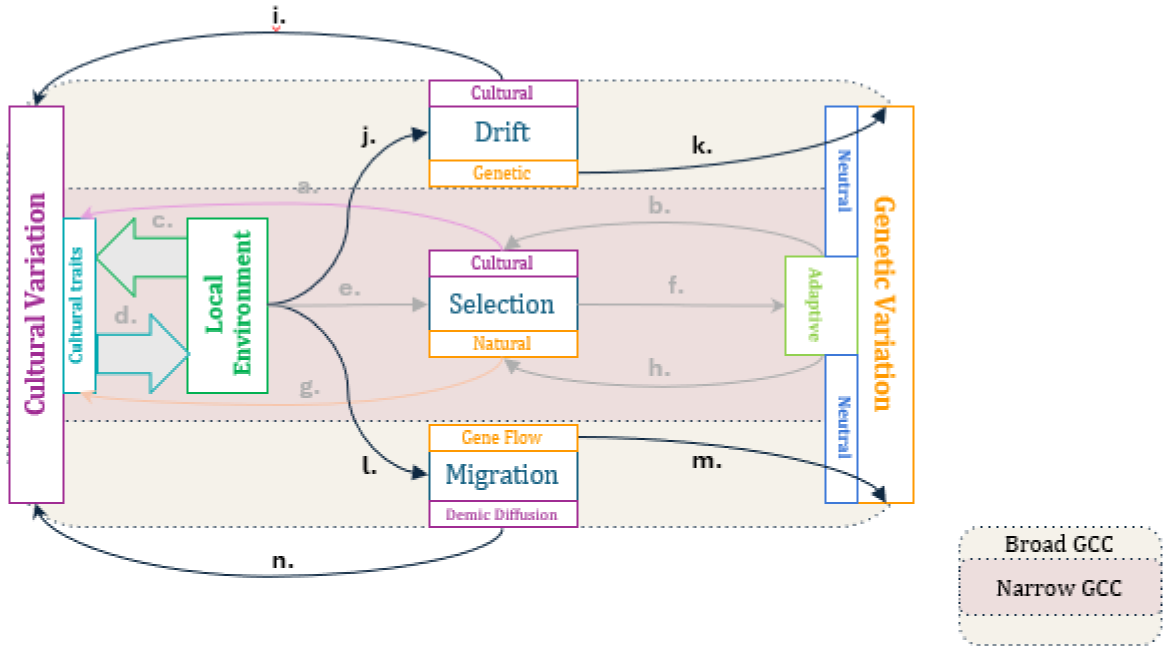

Figure 2: **Illustrative causal diagram for broad gene-culture coevolution.** In addition to the processes outlined in Figure 1, we extend the framework to include the following: i.) cultural drift, j.) eco-cultural and demographic background conditions of genetic drift (e.g. environmental carrying capacity and population size), k.) genetic drift, l.) eco-cultural and demographic background conditions of migration (e.g. geographical barriers and the cultural knowledge needed to overcome them), m.) gene flow, n.) demic diffusion (i.e. movement of cultural traits through movement of people).

2.2 Broad gene-culture coevolution

Broad gene-culture coevolution accepts these core gene-culture interactions but extends them by incorporating two additional evolutionary mechanisms that shape both cultural and genetic variation: drift and migration (see Figure 2). More specifically, broad gene-culture coevolution formally recognises that eco-cultural dynamics can not only influence selection, but may also shape gene and cultural trait frequency changes that arise through drift and migration. There is strong molecular evidence to suggest that neutral evolutionary forces like drift and gene-flow have likely played a pervasive, even predominant, role in shaping extant patterns of human genetic variation (Ramachandran et al. 2005; Williamson et al. 2007; Simon and Coop 2024). This is not to say selection, both positive selective sweeps and pervasive background selection, is unimportant in explaining genetic variation and adaptation in humans (McVicker et al. 2009; Hellmann et al. 2008; Schrider and Kern 2017; Cai et al. 2009; Murphy et al. 2022). Some studies even suggest that linked selection (i.e. selection on genomic regions which are physically adjacent to actual targets of selection) may affect as much as half of the human genome (Schrider and Kern 2017), though others place this number at a much more conservative ~10% (Williamson et al. 2007). But even the extreme case here implies that at least half, and probably substantially more, of human genetic variation is dominated by non-selective processes. Additionally, what these studies have in common in that they rely on contemporary genomic data to attempt to make these complicated inferences. Conversely, Simon and Coop (2024) decompose the contribution of gene flow, drift and selection to allele frequency shifts between both ancient (~5000 years bp) and contemporary European genetic samples. They conclude that gene flow (especially from Yamnaya Steppe pastoralists) and drift account for virtually *all* changes, leaving wide-spread selection only a marginal explanatory role. In light of these results, a theory of gene-culture coevolution that brackets out neutral processes appears unnecessarily limited in its explanatory potential.

The recent Simon and Coop (2024) study illustrates this elegantly. Both the time frame and geography of this work broadly mirror the evolutionary context of the European lactase persistence example (i.e. Central Europe over the last 5000 years). Yet in Simon and Coop's study, this narrowly localised (at the genetic level) selective event, one of the strongest we have evidence for in the human genome, leaves virtually no detectable pattern on overall genetic variation. This is to say - narrow gene-culture coevolution here explains the emergence of a particular phenotype, lactase persistence, but not the wider patterns of genetic variation surrounding it. Those patterns appear to instead be predominantly shaped by an influx of Yamnaya steppe pastoralists into Europe, and the genetic legacy of those migrations (Allentoft et al. 2015, 2024). But what allowed for this influx to happen? More acutely, what cultural traits, perhaps, allowed for the Yamnaya to spread across Europe in the first place (e.g. technological innovations such as wagons, or a pervasive culture of horse riding which enabled their nomadic pastoralism, Anthony 2023)? Broad gene-culture coevolution could set out to explore such questions, and attempt to link cultural patterns to the broad genetic shifts documented by Simon and Coop (2024). Ultimately, ignoring how culturally evolved practices and institutions influence non-selective processes like drift and gene flow necessarily disregards many interesting phenomena, as well as much of the existing empirical literature dedicated to their study.

2.2.1 Drift and gene-culture coevolution

Drift is a stochastic process of allele or trait frequency change that is dependent on effective population sizes as well as the strength of selection, both of which are likely to be profoundly shaped by culture. The fact, noted above, that culture may intensify selection, probably arises both because cultural activities are capable of bringing about unusually rapid, consistent and heritable changes in environmental conditions relative to non-cultural sources of selection (Laland, Odling-Smee, and Feldman 2001), and because (at least in humans) cultural practices have led to striking increases in population size (discussed below). However, the opposite effect is also plausible, with culture leading to relaxed selection on genes. In domains where cultural and genetic traits serve overlapping function, changes in cultural variation may mask functional genetic variation, effectively shielding it from selection and shifting the balance towards drift in determining the dynamics of their evolutionary change (discussed in Durham 1991; Uchiyama, Spicer, and Muthukrishna 2021; Waring and Wood 2021). Interestingly, as the relevant mechanism here still primarily concerns changes in selection coefficients, this particular aspect of drift-like gene-culture coevolution can be construed to be sufficiently covered by “narrow” gene-culture coevolution (e.g. Durham 1991). In practice, however, investigating relaxed selection is only seldom the declared aim of (empirical) gene-culture coevolutionary work.

Furthermore, outwith the narrow approach, the relative strength of random genetic drift (over selection) is also a function of the effective population size of reproducing individuals (Hartl and Clark 2007; Charlesworth 2009), which may similarly be subject to eco-cultural influence. Subsistence transitions, for example, have likely facilitated substantial and rapid increases in population size and density since the mid-to-late Pleistocene by modifying environmental carrying capacity Macpherson et al. (2004). The genetic signatures of such subsistence transitions is evident even in some populations that transitioned from hunting and gathering to agriculture within the last millennium (Padilla-Iglesias and Derkx 2024). It is worth noting here that the action of drift may feed back on both genetic and cultural variation (Figure 2). This is because stochastic variation in transmission is likely also to influence cultural evolution, with analogous underlying factors: Population size, for example, likely plays a role in the preservation of cultural variation and in the efficacy of cultural evolution to generate successful phenotypes (Henrich 2004; Strassberg and Creanza 2020). Additionally, genetically evolved traits may release cultural variation from selective constraints (e.g. via genetic assimilation, Waddington 1942, 1953). In this way, a gene-culture coevolutionary theory of drift still encompasses a fundamentally reciprocal model of cultural and genetic evolution.

Example: Cultural buffering against genetic selection - Vitamin D-folate theory of skin pigmentation evolution, material culture and subsistence Skin tone in humans is a well-documented phenotype with remarkable geographic variation (Yamaguchi and Hearing 2009; McNamara et al. 2021; Jablonski 2004). Biologically, it is function of the distribution of melanosomes in the skin, intracellular organelles generated by pigment cells, which synthesise and store melanin pigments (Lin and Fisher 2007). The most prominent adaptive hypothesis in regard to its evolution, the “Vitamin D” or “Vitamin D-Folate” theory (Jones et al. 2018; Jablonski and Chaplin 2010; Jablonski 2021; J. Liu, Bitsue, and Yang 2024), argues that this variation (and resulting geographical clines) is fundamentally driven by a trade-off between two interacting selective processes, which jointly adjust levels of constitutive pigmentation to reflect (or, more precisely, *absorb*) environmental levels of UV radiation (UVR): Highly pigmented skin may be favoured in UVR-intense environments (i.e. equatorial latitudes) due to the photoprotective properties of eumelanin-rich skin against the depletion of important light-sensitive metabolites (including Folate, Branda and Eaton 1978). Conversely, more sparsely pigmented skin may be favoured in UVR-low environments (i.e. higher latitudes) to allow for more efficient photosynthesis of cutaneous Vitamin D (Murray 1934; Loomis 1967; Jablonski 2021), generally thought to be a crucial nutrient in a wide of physiological processes (Lips 2006, 2007), and conferring protection against certain diseases, such as rickets (Holick 2006). In this account, it is that delicate balance between protective and permissive properties of human skin in relation to UVR that gives rise to the high levels of phenotypic variation observed in contemporary human populations, and its apparent distribution along latitudinal clines (Jablonski and Chaplin 2010).

More recently some researchers have suggested that the evolution of human skin pigmentation is best understood as a biocultural process, rather than a purely biological one (Jablonski 2021; Pryor and Lindo 2023). These biocultural approaches emphasise how cultural traits interact with both of the aforementioned phenotypes (UV protection and Vitamin D synthesis), modifying the respective strength of their selection (and ultimately, the selection of the underlying genetic variation). For example, the evolution of photoprotective material culture, such as various forms of clothing and its attendant production processes, may have modified whether pigmentation itself was necessary to protect against UVR (Jablonski 2021; Lautenschlager, Wulf, and Pittelkow 2007). Along a similar line of argument, Rifkin et al. (2015) hypothesise that habitual skin application of ochre, a naturally photoprotective pigment made from clay, may have served early humans as a kind of early topical "sunscreen" (in addition to ritualistic use), allowing for dispersal into more UV intense habitats and reduced selective pressure from UVR.

An analogous biocultural argument can be made for Vitamin D synthesis. Cutaneous synthesis is not the only (or even primary) source of Vitamin D for the human body - much of it is dietary. Therefore, the relative (fitness) benefit gained from photoactive cutaneous Vitamin D synthesis may partially depend on the amount of Vitamin D intake available via the diet. Culturally evolved subsistence practices modulate the dietary intake of Vitamin D, (de)emphasising the relative importance of cutaneous production in maintaining "healthy" levels. This may explain why dietary shifts to agricultural diets poor in Vitamin D at the start of the Neolithic are sometimes thought to have exacerbated recent selection of depigmented skin (Marciniak and Perry 2017; Wilde et al. 2014; Richards, Schulting, and Hedges 2003). In another example for the possible role of subsistence, strong facultative pigmentation (i.e. "tanning", functionally convergent but mechanistically distinct from constitutive pigmentation) is highly prevalent in some contemporary aquatic hunter-gatherer populations like the Inuit, despite their settlement in extreme latitudes (Jablonski 2021). This been put forward as possible evidence for the role of dietary Vitamin D in the evolution of skin pigmentation, as many of these cultures have traditionally relied on a particularly fishing-heavy diet (Sharma 2010). Fish, particularly fatty fish, represents one of the primary dietary sources of Vitamin D (Lamberg-Allardt 2006). This ample dietary supply, in turn, may have relaxed selection favouring depigmentation in some of these populations (Jablonski 2021). Due consideration of cultural factors such as dietary practices may shed further light on other examples where latitude alone is insufficient in explaining phenotypic variation in skin colouration, including in Native American, European and Asian populations (Quillen et al. 2019). Should further research in that regard mirror existing work, this could represent one interesting example of gene-culture coevolution between cultural (dietary intake) and genetic (cutaneous production) influences on a crucial phenotype (Vitamin D synthesis), where cultural factors may act to buffer selection on genetic variation.

2.2.2 Migration and gene-culture coevolution

Migration (or, in the genetic case, gene flow) is the other evolutionary mechanism that merits integration into gene-culture coevolutionary approaches. Perhaps one of the most remarkable features of the human species is its relatively rapid and pervasive dispersal out of Africa and around virtually all of the globe (Cavalli-Sforza, Menozzi, and Piazza 1996). The peopling of the world, now extensively traced through genomic as well as archaeological evidence, is a direct testament to human mobility and adaptability to novel environments, both of which are likely to be fundamentally enabled and enhanced through cultural traits and systems (Bell 2023; Kuhn, Raichlen, and Clark 2016). While species obviously don't need culture to migrate, there is little doubt that cultural innovation, expressed in knowledge of migration pathways, navigation methods (Fernandez-Velasco and Spiers 2024), modes of transportation (e.g. Anderson 2008), communication, subsistence and general problem-solving capabilities have greatly enhanced, but also occasionally hindered, the potential for human populations to move, and particularly to cross major geographical barriers such as oceans, mountain ranges and deserts (Bell 2023).

It stands to reason that this same set of cultural traits has made modern humans as deeply interconnected a species as it is a mobile and widely dispersed one - indeed, contemporary genomics has repeatedly shown that extensive patterns of expansions followed by inter-population gene flow and admixture have given rise to the remarkably continuous nature of human genetic variation (Nielsen et al. 2017). As before, the action of this pervasive migratory tendency clearly affects both cultural variation (e.g. via demic diffusion of cultural traits) and its genetic counterpart (via gene flow and admixture). And as before, patterns of migration are likely deeply shaped by various eco-cultural forces influencing the modes, pathways and impetuses of migration - navigational traditions modifying migratory reach (Bell 2023; Kuhn, Raichlen, and Clark 2016), linguistic barriers or trade networks channeling the flow of migratory individuals (Barbujani and Sokal 1990), or post-marital residence norms regulating which sex disperses (Oota et al. 2001). Clearly, the role of culture in the dynamics of these processes is profound - yet studies of its impact have in the past largely been excluded from the thematic umbrella of gene-culture coevolution.

Example: Culture shapes the pathways of migration - Trade networks shape gene flow in Melanesia, and vice versa Arguably, one compelling example of the gene-culture coevolutionary dynamics of migration has been a well-known part of the anthropological canon for the better part of the last century. In 1922, anthropologist Bronislaw Malinowski (1922a) published *Argonauts of the Western Pacific*, a now classic ethnography principally focused on the people of the Trobriand Islands in the Massim region off the eastern coast of Papua New Guinea (PNG). Much of this work is dedicated to a painstaking retracing of the *kula*, a (roughly) ring-shaped network of gift exchange spanning both linguistic and cultural boundaries across the entire region and adjoining the eastern tip of PNG with its outlying archipelagos. *Kula* societies exchange valuables, notably shell necklaces (*soulava*) and armbands (*mwali*), with specific trading partners to either side of their position in the ring, creating an intricate and seemingly historically deep system of circular gift exchange that remained in place, even flourished, long after European contact, and into the present day (Malinowski 1922b; Persson 1983; Leach and Leach 1983).

The functional and symbolic intricacies of the *kula* (or perhaps *kula*-ing, as *kula* is a verb in the local languages) have received much attention over the decades following Malinowski's original description, and later anthropologists were quick to point out that it represents, in part, a kind of abstraction of deeper inter-cultural networks of trade and alliances existing in the region (Leach and Leach 1983). All manner of resources are said to have followed the flow of the *kula* ring - shells, trade goods and people alike. Similarly, the concept of the *kula* itself, and the associated rites and myths, seem to have spread and reinforced across the region in a clear examples of cultural transmission (Irwin, Shaw, and Mcalister 2019). Additionally, the configuration and constancy of the *kula* ring were likely shaped by a rich mosaic of cultural and ecological factors, including winds, island ecology and maritime technologies - pointing towards the deep importance of a whole range of culturally evolved factors (Irwin, Shaw, and Mcalister 2019).

What might a gene-culture coevolutionary hypothesis for the *kula* look like, if based principally on gene flow as the mechanism of interest? Chiefly, we might expect populations connected through the network to be more closely related genetically than geographic distance alone would suggest, as the *kula* may facilitate gene flow (in the form of migration and intermarriage) and subsequent homogenisation between these populations. While population genetic studies of the region are few and far between, the two studies that do exist render such a connection highly plausible. One study by Oven et al. (2014) examined patterns of paternally inherited Y-chromosomes (NRY) and maternally inherited mitochondrial DNA (mtDNA) across the Massim region. Notably, this study included both island populations that traditionally participate in the *kula*, as well as some that do not (although such categories are difficult to establish given the intrinsically flexible nature of the *kula* emphasised by anthropologists). Two results stand out in evaluating the potential role of the *kula* in directing gene-flow in the region: Firstly, both NRY and mtDNA data suggested that local genetic structure is best explained by a rough division of the region into a northwestern group (consisting of islands that traditionally participate in the *kula*), a southeastern group (consisting of islands that traditionally do not participate), and Rossel Island (a traditionally endogamous culture on the very southeastern tip of the Massim). This finding implicates the network as a mechanism of differentiation.

The second finding, perhaps even more remarkable, comes from examining NRY and mtDNA data separately. Here, evidence suggests that kula-trading populations show relatively clear population differentiation (roughly as predicted by the isolating effects of distance) in their mtDNA, *but not* their Y-chromosomal DNA. This is to say that male-inherited genetic diversity is *much* more genetically homogenous across the *kula*-ring than is female-inherited genetic diversity. It is important to consider here that *kula* voyages were traditionally predominantly performed by men (Leach and Leach 1983), so a plausible hypothesis may be that *kula*-mediated male gene-flow has given rise to these patterns. Notably, the few Massim region cultures included in cross-cultural datasets like the Ethnographic Atlas are coded as virilocal (i.e. effectively patrilocal, suggesting female migration), in line with the overwhelmingly patrilocal traditions of wider PNG (Jordan et al. 2009) - but the pattern observed in the Massim runs exactly counter to the expectation for patrilocal groups (Oota et al. 2001), rendering post-marital residence norms an unlikely alternative explanation. Overall, Oven et al. (2014) make a strong case for role of the *kula* in affecting the genetic structure of the Massim.

Subsequently, D. Liu et al. (2022) analysed genome-wide data of 192 individuals across 15 groups to further elucidate the genetic structure of the Massim region. Instead of genetic distance, they examine patterns of IBD sharing (shared tracts of DNA between individuals that indicate common descent, often used to infer migration) to interrogate a potential role for the *kula* in shaping the regions genetic structure. D. Liu et al. (2022) found higher IBD sharing among *kula*-participating islands than among those excluded from the traditional network, indicating, again, a potentially facilitative role of the exchange network. Notably, however, they infer for these patterns to have time depth of thousands of years, predating archaeological evidence of the kula by some time (Irwin, Shaw, and Mcalister 2019). They offer two non-exclusive explanations for the observed pattern: for one, it is likely that the although the *kula* tradition itself may be a relatively recent phenomenon, it reflects a network of trade and alliance partners of considerable deeper chronological depth (Shaw 2016; Shaw and Langley 2017). Secondly, and particularly appealing to the reciprocal nature of coevolutionary approaches, D. Liu et al. (2022) speculate that it may, in part, have been the connectivity, shared ancestry and geneaological connection between the islands of the Massim region that gave rise to the *kula* system - a case, perhaps, of genetic affinity leading to a self-reinforcing cultural practice (or genes influencing culture in an unusual and indirect way), and a striking illustration of non-adaptive gene-culture coevolutionary dynamics.

2.3 Gene-culture coevolution reconsidered

Having laid out a case for this expanded definition of gene-culture coevolution, it is worth discussing how we believe this taxonomy differs from some other attempts at organising related research, starting with more recent work. Waring and Wood (2021) specify three "modes" of gene-culture coevolution - trait-pair coevolution (more in line with narrow-sense coevolution), trait-system coevolution, and system-system coevolution. "System" here refers to inheritance systems, i.e. cultural or genetic inheritance. *Trait-pair* coevolution describes the "classic" reciprocal changes between a cultural trait and a genetic one, i.e. a cultural trait altering the fitness of a certain genetic trait, and *vice versa.* Trait-system coevolution describes the influence that single traits in one domain can have on the entire inheritance system in the other. Finally, *system-system* coevolution describes a scenario where having two separate (and mechanistically distinct) pathways for (adaptive) evolution may lead to one system "crowding out" the other. While very useful and encompassing many gene-culture interactions that we also suggest should be included in the gene–culture coevolutionary framework, this approach is more concerned with categorising the respective targets (or levels) of reciprocal change, rather than the evolutionary mechanisms through which such targets interact. Therefore, it represents a useful, but orthogonal rather than rivaling, approach to our mechanism-focused taxonomy.

A classic attempt at categorising gene-culture interactions comes from Durham (1991). In fact, Durham (1991) originally proposed the same narrow / broad gene-culture coevolution terminology that we have introduced here. However, Durham's approach seems fundamentally disinterested in the role of what he calls "nonconveyance forces" in both genetic and cultural evolution, which include mutation, innovation, migration, and drift. Consequently, the narrow / broad dichotomy Durham (1991) proposes as the framework for understanding gene-culture coevolution is exclusive focused on reciprocal fitness changes between genetic and cultural traits, and the directionality of these changes (i.e. degree of concordance between the cultural and genetic fitness effects of relevant traits) - bracketing out "nonconveyance forces" entirely.

Following earlier research on whales suggesting that culture could shape neutral genetic variation and account for low genetic diversity Whitehead, Vachon, and Frasier (2017), Whitehead and colleagues (2019) proposed a broader conception of gene-culture coevolution roughly in line with our own. Like those authors, we propose that understanding and defining gene-culture coevolution in this *broad* sense, which includes those nonconveyance forces and the role that cultural and genetic variation play in shaping them, is the most fruitful approach to get to the core of what we suspect most gene-culture coevolutionists are interested in - namely, understanding the full extent of the role that culture and cultural evolution have played in shaping genetic evolution in general, not just adaptive genetic evolution.

Despite this plea for mechanistic and conceptual inclusivity, however, it is important to consider where we lay the boundaries for this broader definition of gene-culture coevolution. As Thompson (1989) notes in his breakdown of the use of the term "coevolution" in evolutionary biology, the word potentially "loses its utility when it is applied so broadly that all possibility of analysis of the mechanisms of reciprocal change is lost" (p. 181). This is equally true in the case of gene-culture coevolution. A cohesive definition must be bounded, or it runs the risk of being diluted to the point of incoherence. For the purposes of clarity, it is useful to reconsider some previous misgivings with the imprecise use of "coevolution" in evolutionary biology (Janzen 1980). Like those critics, we believe it is important to distinguish between *evidence of interaction* and mere *mutualistic congruence,* i.e. patterns of correspondence that are not due to reciprocal influence. We contend that there are (at least) two processes which may lead to such patterns which warrant consideration in the gene-culture case - and the distinction between these two processes gets to the core of a consistent definition of gene-culture coevolution.

The first process, described by Janzen (1980), is a correspondence that is due to matching of compatible traits that were already present in coevolving organisms, rather than brought about by reciprocal change. For example, seemingly matching phenotypic traits in predators and prey may stem from the fact that predators in a new environment *selected* the prey most suited to be exploited by their existing phenotype, rather than evolving a phenotype tailored towards that prey. Such "matching" may also occur in gene-culture coevolution - a certain cultural trait may establish itself so as to match existing genetic traits, for example material culture evolving to match physiology. Unlike Janzen, however, we propose that for our purposes this *is* indeed a coevolutionary phenomenon - the nature of one trait influences form and formation of another, e.g. via cultural selection. This is, in part, a practical consideration - though often plausible, truly reciprocal relationships between genes and culture are difficult to pinpoint empirically as this would require some way of tracking change in both systems across evolutionary time. But more broadly, whether this causal relationship becomes reciprocally reinforcing is, at this point, of secondary importance. Unlikely as it is, even a purely unidirectional relationship tells us something about how genes and culture come to interact and correspond. This effectively relaxes, if not entirely abandons, the reciprocity requirement of the coevolution definition (in line with Whitehead et al. 2019).

The second process which may lead to correspondence between genetic and cultural variation derives from the idiosyncrasies of a dual-inheritance system, and may help us demarcate what does *not* constitute gene-culture coevolution. Consider a cultural trait that is transmitted vertically across generations, from parent to child. Through time and space, the history and spread of this trait may almost directly mirror the history and spread of genes, as it travels in parallel with genetic information (Cavalli-Sforza and Feldman 1973). Affected equally by demographic change, migration and founder effects, geographical patterns of genetic and cultural variation may come to correspond, yet nowhere in this hypothetical scenario do the traits actually interact, in the sense of influencing eachother's transmission - they are merely inherited together. As noted early on by Cavalli-Sforza and Feldman (1981), this renders such correlations between cultural and genetic variation spurious rather than causally meaningful. In the study of genetic and cultural variation, the possibility of such "parallel transmission" scenarios is most clearly exemplified by the relationship between linguistic and genetic lineages. Numerous ambitious studies, for example constructing co-phylogenies from linguistic and genetic data, have shown that there is a clear patterns of similarity between linguistic and genetic diversity in humans (Cavalli-Sforza et al. 1988; Penny, Watson, and Steel 1993; Sokal 1988; Barbieri et al. 2022). One line of thought is that these patterns stem from parallel transmission of language and genes - via processes like "local codiffusion" (i.e. concurrent *horizontal* transmission) or simply the aforementioned parallel vertical transmission (Barbieri et al. 2022). We believe such phenomena constitute a useful boundary for gene-culture coevolution - if culture and genes merely travel together, but do not influence eachother's spread or dynamics, *this does not constitute gene-culture coevolution.* Causal interaction through any given evolutionary mechanisms, even if it is unilateral, should be the defining property of gene-culture coevolution. It is worth noting here that the gene-language coevolution literature indicates that this hypothetical "perfect parallel transmission" scenario is likely rather transient in human populations, partially because language often evolves much faster than genes. Over longer timespans, as Barbieri et al. (2022) point out, linguistic and genetic lineages sometimes seem to give largely non-overlapping accounts of divergence times, leading the authors to assert that instead, preceding genetic diversification may trigger cultural diversification down the line, whereas early linguistic diversification may cause barriers to gene flow which affect genetic structure. Both of these scenarios, in turn, would indicate coevolutionary mechanisms that satisfy our simple criterion of non-independent co-inheritance. Nevertheless, parallel transmission may represent a useful null model for empirical investigations of gene-culture coevolution where correspondences between genetic and cultural variation are observed. Notably, such patterns are still interesting and meaningful - for example, in the interpretation of genome-wide association studies (GWAS), which may be confounded by the independently co-inherited genetic and cultural traits whose relationship is not actually causally relevant (Feldman and Ramachandran 2018). Overall, such a null-model of independent co-inheritance speaks to our core motivation behind proposing this framework.

3 Conclusions: a science in progress

By focusing on mechanisms of evolutionary change, we hope the framework proposed here will benefit the field in two ways; looking back and looking forward. For one, we believe this expanded definition may serve to reframe a significant amount of deeply insightful existing research as being perfectly consistent with, or even supportive of, gene-culture coevolution as a theoretical framework. This work, despite not being explicitly framed as gene-culture coevolution perhaps in part due to its focus on non-selective phenomena, has done much to showcase the deep influence of cultural phenomena on human genetic variation. Its full extent deserves a review in itself, but a non-exhaustive list may include genetic structure being shaped by linguistic boundaries (Barbujani and Sokal 1990; Balanovsky et al. 2011; Pichkar and Creanza 2023), post-marital residence norms (Oota et al. 2001), subsistence transitions (Padilla-Iglesias and Derkx 2024), assortative mating (Yengo et al. 2018; Robinson et al. 2017), culturally-determined social stratification (Moorjani et al. 2013; Basu, Sarkar-Roy, and Majumder 2016), or endogamy and consanguineous marriage norms (Bittles and Black 2010). More importantly, and looking to the future, we hope this framework may open new avenues of theoretically motivated empirical research on gene-culture coevolution going forward. By using a broader selection of well-established evolutionary mechanisms or forces as the organising principle for gene-culture interactions, broad gene-culture coevolution may provide a promising and simple way of generating novel causal hypotheses on the reciprocal influences of cultural and genetic variation. In other words, by specifying the “rules of engagement”, it may allow us to move from an associative to a causal understanding of genetic and cultural data (Pearl 2009), for example through the generation of causal models (e.g. illustrated through directed acyclic graphs or DAGs) based on analogous and well-studied environmental influences on genetic structure. This can then be used to form empirically testable expectations around cultural influences on genetic structure firmly rooted in the evolutionary theory in which our broad approach to gene-culture coevolution is embedded. Empirical work on gene-culture coevolution is undoubtedly tricky, as both domains must be treated with the nuance required by their respective complexities. As such, the vision of gene-culture coevolution laid out here is a, fundamentally, an interdisciplinary and conciliatory one: A richer empirical science of gene-culture coevolution will require a unique synthesis of anthropology, archaeology, cognitive sciences, ecology, developmental and evolutionary biology, genetics, genomics, history and mathematics - not necessarily all at once, but with each discipline having a substantial role to play in unraveling the intricate causal mechanisms proposed here (see also Zeder 2018). Burgeoning methodological advancements in the integration of cross-cultural and archaeological data with genetic research, for example, promise to drive deeper understanding in the field (e.g. Evershed et al. 2022).

This approach also dispels the notion that gene-culture coevolution is strictly a rival theory to other approaches in the evolutionary human sciences. Rather, we propose it as an overarching framework, the constituent parts of which can be investigated using any number of approaches. This includes human behavioural ecology (e.g. examining the relationship between cultural traditions and ecology, Micheletti et al. 2023), evolutionary psychology (e.g. examining how biases toward certain cultural traits and the cognitive machinery of social learning emerge in the first place, Mesoudi 2009), and of course cultural evolution itself. As such, we are sympathetic to other recent work that has similarly argued for some conceptual rearrangement and synthesis (Micheletti, Brandl, and Mace 2022; Micheletti et al. 2023).

However, we lay no claim to having devised an immutable theory of gene-culture coevolution - quite the opposite. For one, even this expanded approach privileges selection, drift and gene flow as the primary evolutionary mechanisms of gene-culture interaction, but it need not do so. Indeed, there are any number of other mechanisms that could, and have been, construed to be evolutionary processes - most notably mutation, but also recombination or assortative mating (e.g. Mayr 2002; Posada, Crandall, and Holmes 2002). It is conceivable that cultural influences may play a role in those domains as well. For example, given the well-established role of parental ages on the human germline mutation rate (Gao et al. 2019; Girard et al. 2016), it is possible kinship norms regulating age-at-marriage or age-at-first-birth play a measurable role in the emergence of population-level differences (either across space or time) in mutation rates (but see Gao et al. 2023). In the future, the argument could be made that nascent work on those kinds of questions may also productively fit within a gene-culture coevolutionary framework (Figure 3).

Similarly, there are a number of coevolutionary phenomena that fall within our broad conceptual framework, but (largely) outside of the scope of what has been presented here. In evolutionary biology, coevolution is often an interspecific process (Janzen 1980) - and there is virtual certainty that human culture has dramatically influenced the evolution of many species that we share environments and ecosystem with, including both animal and plant domesticates (Hendry, Gotanda, and Svensson 2017). To stick with gene-culture coevolution's flagship example, new evidence suggests for instance that lactase persistence alleles have also been selected for in European dogs (Y.-H. Liu et al. 2021). Overall, the influence of human culture on non-human genetic evolution, and vice versa, is causally intricate and likely ubiquitous (e.g. via artificial selection, Conner 2003; Meyer, DuVal, and Jensen 2012). This doubtlessly opens many avenues for scientific inquiry, including how

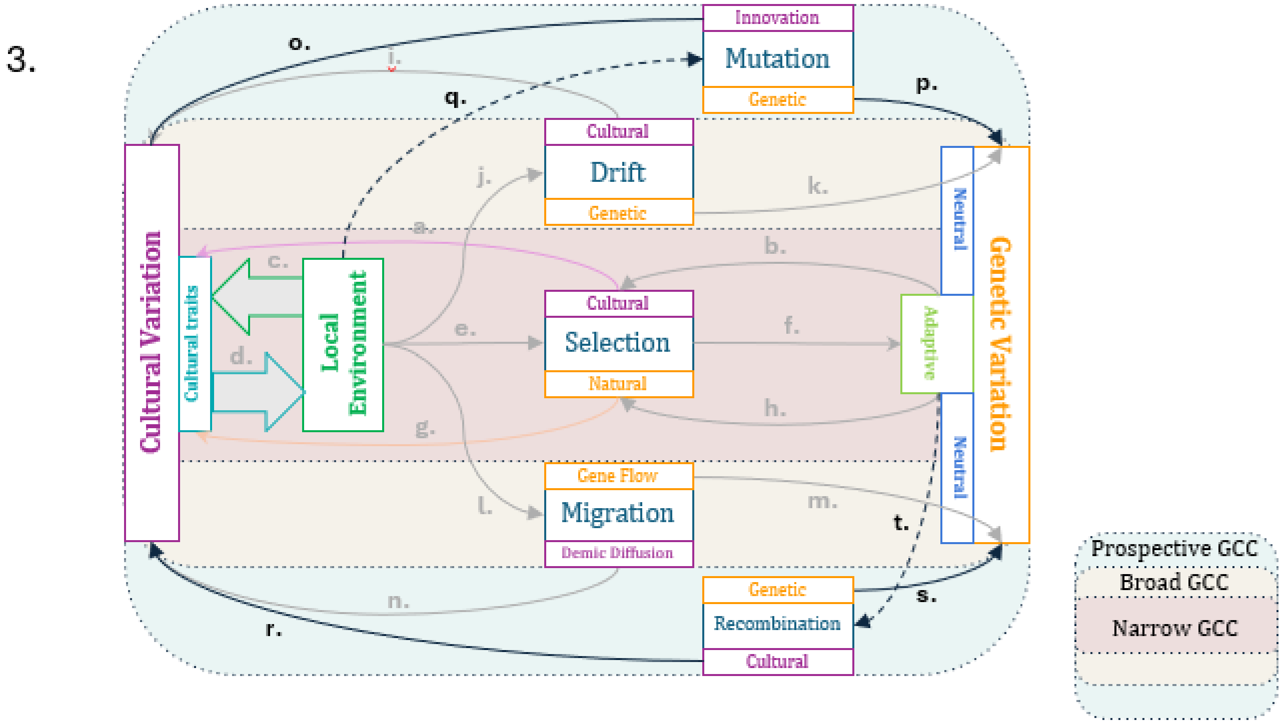

Figure 3: **Potential areas of future research on gene-culture interactions.** Conceivably, there are gene-culture coevolutionary processes beyond those outlined in previous figures, concerned with additional candidate mechanisms that we have sidelined. Some plausible causal links, suggested from adjacent literature, are represented through dashed lines. o.) Mutational processes in cultural evolution, i.e. innovation, generating novel cultural variation, much like, p.) mutational processes in genetic evolution generating novel genetic variants, q.) the eco-cultural environment shaping both of those processes, e.g. through social network structures favouring innovation, or through reproductive processes affecting the average germline mutation rate across populations, r.) cultural recombination generating new cultural phenotypes by recombining existing cultural traits across lineages (e.g. Creanza, Kolodny, and Feldman 2017), s.) genetic recombination generating novel haplotypes, t.) evolved genetic traits affecting the speed and extent of recombination for both genetic variation (e.g. recombination rate evolution) and cultural variation (e.g. evolved cognition).

the spread of certain cultural traits may correspond to the genetic structure of many domesticated organisms, which may benefit from an explicit gene-culture coevolutionary framework. The same goes for considerations of gene-culture coevolution beyond the human domain: The study of 'animal cultures', socially acquired behavioural traditions in non-human animals, is a growing science (Laland and Hoppitt 2003; Whiten 2021; Schuppli and Schaik 2019). There is now rapidly accumulating evidence that the same causal interactions that mark human cultural and genetic evolution may lead to gene-culture coevolutionary phenomena in non-human animals as well (Whitehead et al. 2019), spanning the animal kingdom from cetaceans to insects (Whitehead 2017; Bridges and Chittka 2019). The applicability of a gene-culture coevolution framework outside of human evolution should help to ground the theory in the broader canon of evolutionary biology.

We hope that the current discussion, as well as the examples we elected to illustrate it, goes some way to make the case for a broader science of gene-culture coevolution that would allow us to paint a more vivid picture of all the causal interactions between genes and culture. The empirical investigation of gene-culture coevolution remains a fledgling scientific effort, but our sincere hope is that the rigorous theoretical framework in which gene-culture coevolution has originally been conceived, thus expanded upon, may prove to be useful guiding theory for the study of biocultural human evolution across disciplines, including anthropology - whose nuanced understanding of the breadth and depth of human culture is central to such efforts (see also Wiley and Cullin 2016). Because ultimately, it will take surely take a concerted, cross-disciplinary effort to answer this one simple question - how, and to what extent, have humans shaped their own evolution?

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