Not by selection alone: expanding the scope of gene-culture coevolution

Sven M. Kasser[1]*, Kevin N. Lala[1], Laura Fortunato[2], Marcus W. Feldman[3]
[1]School of Biology, University of St Andrews, St Andrews, United Kingdom
[2]Institute of Human Sciences, University of Oxford, Oxford, United Kingdom
[3]Department of Biology, Stanford University, Stanford, California, USA

*Corresponding author: Sven M. Kasser; `sven.kasser@gmail.com`

Abstract

Gene-culture coevolution (GCC) - an ambitious synthesis of biological and social sciences - is often used to explain the evolution of key human traits. Despite the framework's broad conceptual appeal however, empirical evidence is often perceived as limited to a few key examples like lactase persistence. We argue this apparent gap between theoretical appeal and empirical evidence stems from conceptual ambiguities regarding the scope of relevant gene-culture interactions. Drawing on recent work in animal gene-culture coevolution and human genomics, we propose a "broad" approach that formally incorporates drift and migration alongside natural selection. This builds upon and subsumes the existing "narrow" framework focused on selection. Through case studies of skin pigmentation evolution and gift-exchange network influences on genetic variation in Melanesia, we demonstrate how cultural factors shape both adaptive and neutral genetic variation and population structure. This integrative perspective accommodates diverse empirical findings while opening new avenues for research in human evolution.

Keywords: gene-culture coevolution, cultural evolution, population genetics, human evolution, social learning

1 Introduction

A new perspective on human evolution has emerged over the past fifty years that attempts to integrate insights from the "natural" and "social" sciences into a comprehensive formal framework that can explain the distinctive 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 systems that often result in (adaptive, but occasionally maladaptive) phenotypic change over time (Aoki, 2001; Cavalli-Sforza and Feldman, 1973,8; Durham, 1991; Feldman and Cavalli-Sforza, 1984; Richerson and Boyd, 2005; Richerson et al., 2010).

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 widely accepted (McGue and Bouchard, 1998; Nisbett et al., 2012; Uchiyama et al., 2021). The study of such interactions is not exclusive to gene-culture coevolutionary theory; it is also important, for example, in the quantification of gene-environment interactions and the analysis of correlations between relatives (see Hunter, 2005; Manuck and McCaffery, 2014). However, the evolutionary significance of this interplay can be elucidated through a theoretically rigorous and empirically grounded science of gene-culture coevolution.

The central concepts of gene-culture coevolution have changed relatively little since its inception through the pioneering work of Cavalli-Sforza and Feldman (1973,8), and later Boyd and Richerson (1985). At its core, it shares with broader cultural evolutionary theory a commitment to the idea that the population-level transmission dynamics of cultural information mimic those of biological evolution sufficiently to allow for an evolutionary framework of cultural change Mesoudi (2011). But beyond that, it focuses on the possible *interactions* between the two systems of inheritance, i.e., 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 (a process known as cultural niche construction, see e.g. Denton et al., 2023; Ihara and W. Feldman, 2004; O'Brien and Laland, 2012).

Another common definition of (gene-culture) coevolution is more closely aligned with the use of the term 'coevolution' in evolutionary ecology (Janzen, 1980). This more demanding interpretation invokes a deeper causal interdependence between the coevolving elements - or, more precisely, *dynamic reciprocal evolutionary change*, usually 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 biological and cultural evolutionary processes interact through mutual causal feedback. For instance, 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. At the same time, cultural practices can modify the ecological conditions that drive natural selection on the human genome, including genotypes underlying the traits that enable and amplify enculturation in the first place (Kendal, 2015; Laland, 2017). To account for this interplay between often disparate domains of inquiry, the science of gene-culture coevolution must draw upon a wide range of relevant disciplines, from genetics to cognitive science and cross-cultural anthropology.

Such an ambitious scientific endeavor requires conceptual clarity. In the present paper, we set out to both clarify and expand what researchers traditionally mean by "gene-culture coevolution". We first query the central scientific motivations behind applying gene-culture coevolutionary frameworks and define *narrow gene-culture coevolution*, namely the more traditional and commonly applied approach, before subsequently introducing an expansion of that framework, which we call *broad gene-culture coevolution*. This expanded framework includes non-selective mechanisms, namely drift and migration, into gene-culture coevolutionary theory, which produces a more comprehensive explanatory framework for analyzing recent human evolution. We illustrate the utility of this wider viewpoint with 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 way of a traditional trading network, the Kula ring, may have shaped genetic patterns in Oceania. We conclude by considering the limitations and boundaries of this expanded approach and suggesting a way forward for the wider field.

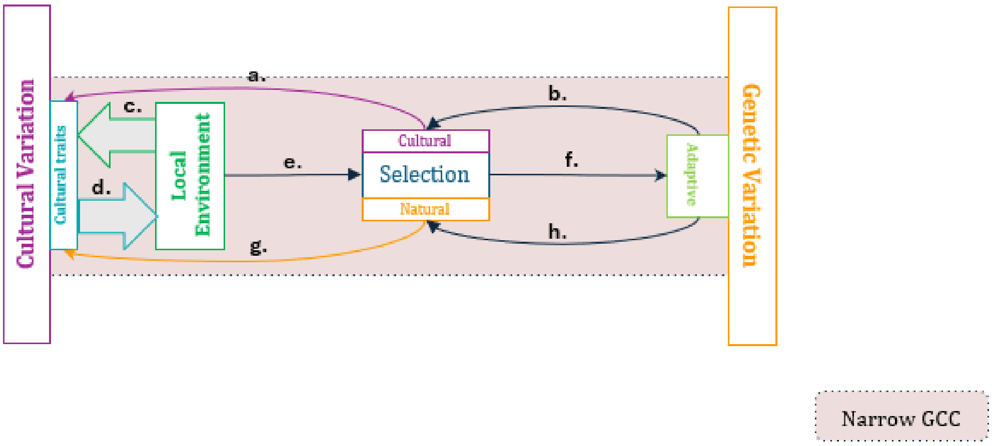

Figure 1: **Causal diagram for narrow gene-culture coevolution.** The arrows here represent the following causal interactions: a.) cultural selection on cultural variation (i.e. the differential transmission and copying of cultural variants, e.g. due to conformist bias), b.) genetically evolved (cognitive) 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-cuture coevolution

2.1 Narrow gene-culture coevolution

Many common definitions of gene-culture coevolution mirror, explicitly or implicitly, the coevolution-through-coadaptation conception that dominates evolutionary ecology. Their originators, among them many of the field's key contributors, appear primarily concerned with gene-culture interactions that lead to "new selective pressures" (Richerson et al., 2010, p8985), to "selection [. . .] generated or modified by [culture]" (Feldman and Laland, 1996, p453), or that become the "basis for genetic selection" (Gintis, 2011, p879). In other words, the focus clearly appears to be on *selective* processes, namely on cases where cultural elements modify the natural selection of genetic variation (the "culture-to-genes" direction of gene-culture coevolution), but where the requirement of reciprocal co-adaptation – i.e., cases where frequencies of associated cultural and genetic variants change together – appears to have been relaxed (see also Whitehead et al., 2019).

Narrow gene-culture coevolution focuses on the reciprocal action of selective processes on both cultural and genetic variation (see Figure 1). Culturally evolved traits and the local ecology can interact to form the selective environment (including tangible and intangible features, e.g., physical geography and social norms). In principle, this interaction is inherently reciprocal. Some cultural traits are adaptive and shaped by the local ecology (Mathew and Perreault, 2015; Micheletti et al., 2023). At the same time, culturally evolved traits can 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 et al., 2003; Kendal et al., 2011; Lewontin, 1989). While the dynamics of these interactions are important topics of research in themselves, the gene-culture coevolutionary framework primarily concerns their outcome, namely, the eco-cultural "landscape" that sets the stage for genetic selection, which affects adaptive genetic variation. Take the flagship example of gene-culture coevolution, lactase persistence (i.e., the ability of humans to digest lactose into adulthood; see Box 1). Here, the eco-cultural dynamics of 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, may affect the incidence and utility of dairying.

More generally, the genetic variation favored by culturally modified natural selection may feed back to shape the selection acting on cultural variation in at least two ways. On the one hand, both cognitive biases towards certain cultural traits (Sperber, 1996; Stubbersfield, 2022) and a psychological bias towards cultural learning (Henrich, 2015; Kendal et al., 2018; Laland, 2017) may evolve and shape the action of cultural selection, namely the biased transmission and spread of certain cultural variants (Richerson and Boyd, 2005). On the other hand, genetic contributions may also influence the fitness, and hence natural selection of individuals with certain cultural traits, or certain variants of a particular cultural trait. In the lactase persistence example, the presence or absence of lactase persistence may have modified the fitness advantage of practicing dairy pastoralism (Gerbault et al., 2011). Taken together with the culturally-shaped selection on genotypes, these two pathways produce the reciprocal feedbacks fundamental to the classic gene-culture coevolutionary approach (see Figure 1).

With its focus on selection, this narrow mode of gene-culture coevolution is often invoked as a framework to explain the form and function of evolved cultural and biological traits, as well as their perceived distinctiveness. In this context, such a selection-focused approach can certainly be productive. Gene-culture coevolutionary approaches to explain such phenotypes as lactase persistence (see Box 1) or even large-scale cooperation and musicality, employ gene-culture coevolutionary theory in this fashion (Chudek and Henrich, 2011; Gintis, 2011; Savage et al., 2021).

BOX 1 Cultural modification of selection

The best known example of narrow sense gene-culture coevolution is the evolution of human adult lactose tolerance and the associated ability to digest dairy products. Most humans (and 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, due to genetic variants in the lactase gene LCT and associated regulatory regions such as MCM6 (Ingram et al., 2009; Lewinsky et al., 2005; Swallow, 2003; Tishkoff et al., 2007). 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 practice that provides a novel abundant source of milk in the diet, may predate this adaptation and may have produced the selection pressure to favor lactase persistence (Aoki, 1986; Feldman and Cavalli-Sforza, 1989; Gerbault et al., 2011; Holden and Mace, 1997; McCracken, 1971; Simoons, 1969). It also showcases the potentially transformative power of gene-culture coevolution, as selection on LCT is estimated to have been some of the strongest selection in the human genome to date (Voight et al., 2006). While this represents a textbook example of gene-culture coevolution (e.g. Durham, 1991), not all details of the lactase persistence story are fully understood, and important aspects (e.g., the strength, timing and mechanisms of selection) are continually revisited and updated as new ancient DNA is analyzed and archaeological evidence emerges (Campbell and Ranciaro, 2021; Ségurel and Bon, 2017). This example highlights the complexity of gene-culture coevolutionary inference even in the narrow sense (see also Evershed et al., 2022).

The evolution of lactase persistence is remarkable in the wide attention and general acceptance it has received in the scientific community as a cross-disciplinary phenomenon (Evershed et al., 2022; Tishkoff et al., 2007), spanning genomics, medicine, anthropology, and archaeology. This prominence has played a key role in reifying the belief 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), which has been posited to be a direct function of the predominantly fishing-based subsistence of these Arctic marine hunters (Deutch et al., 2007; Fumagalli et al., 2015). 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 the subsistence culture (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 (Han et al., 2007; Osier et al., 2002); some variants may result in a protective genetic response to cultural practices such as rice cultivation in East Asia, which gave rise to increased alcohol consumption (Peng et al., 2010). Recent studies of ancient DNA suggest that the number of copies of the amylase gene may also have increased as a consequence of human adoption of agriculture (Bolognini et al., 2024; Yılmaz et al., 2024)

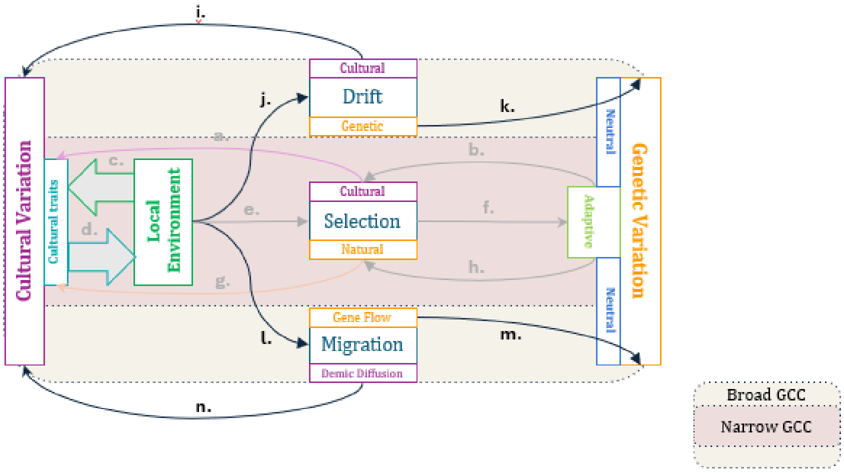

Figure 2: **Causal diagram for broad gene-culture coevolution.** In addition to the processes outlined in Figure 1, this framework includes the following: i.) cultural drift, j.) eco-cultural and demographic background conditions of genetic drift (e.g. environmental carrying capacity and population size), 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

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 *broader* array of gene-culture interactive processes needs to be considered to fully account for the emergence of and change in genetic and cultural variation. In their initial formulation of the cultural evolutionary theory in which gene-culture coevolution is rooted, (Cavalli-Sforza and Feldman, 1981) extensively model the role that neutral evolutionary processes like drift and migration, rather than selection alone, play in shaping not only genetic, but also cultural evolution. However, subsequent works that can be seen as early approaches to gene-culture coevolutionary theory de-emphasize drift and migration as core mechanisms (Boyd and Richerson, 1985; Durham, 1991), and largely adopt the narrow approach outlined above. Only recently has the importance of drift and migration in the explicit context of gene-culture coevolution again been highlighted, notably in work on nonhuman animals, such as whales, where the influence of culture on both adaptive and neutral (i.e. non-selective) evolutionary processes is emphasized (Whitehead et al., 2019).

Why is it important to adopt a similar approach in regard to human gene-culture coevolution? As we describe below, genetic analyses suggest that human biological evolution since the emergence of our species is profoundly affected, if not dominated, by drift, founder effects, and gene flow, rather than natural selection (Ramachandran et al., 2005; Simon and Coop, 2024; Williamson et al., 2007). This implies that a focus on selection alone is unlikely to reveal the full picture, and other evolutionary processes, including (cultural impacts on) mutation, drift, and gene flow, should be included. In fact, it seems highly plausible that the current narrow focus of gene-culture coevolution may inadvertently exclude some of the most important forms of evolutionary interaction between genes and culture in humans. 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 a wider evolutionary context. In short, we believe that approaches to gene-culture coevolution may differ in *scope* (emphasizing selection alone vs emphasizing selection, drift, and migration) because the application of the framework may differ in *purpose* (explaining traits vs characterizing wider evolutionary dynamics).

Broad gene-culture coevolution accepts all the core gene-culture interactions of the narrow framework but extends them by incorporating two additional evolutionary mechanisms that contribute to both cultural and genetic variation: drift and migration (see Figure 2). It formally incorporates eco-cultural dynamics that may 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 such neutral evolutionary forces have played a major, even predominant, role in shaping extant patterns of human genetic variation (Cavalli-Sforza and Feldman, 1981, pp. 109–124, 157–179); (Ramachandran et al., 2005; Simon and Coop, 2024; Williamson et al., 2007). This is not to say that selection, both positive selective sweeps and background selection, is unimportant in explaining genetic variation and adaptation in humans (Cai et al., 2009; Hellmann et al., 2008; McVicker et al., 2009; Murphy et al., 2022; Schrider and Kern, 2017). Some studies even suggest that linked selection (i.e. selection on genomic regions that are physically adjacent to actual targets of selection) may affect as much as half of the human genome (Schrider and Kern, 2017), though other estimates are much more conservative, at 10% or less (Williamson et al., 2007). But the implication is that at least half, and probably substantially more, of human genetic variation is dominated by non-selective processes. Additionally, what many of these estimates have in common in that they rely on contemporary genomic data in making 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 only a marginal explanatory role for selection. In light of these results, a theory of gene-culture coevolution that ignores neutral processes is limited in its explanatory potential.

(Simon and Coop, 2024) illustrate this issue elegantly. Both the time frame and geography of their example broadly mirror the evolutionary context of the European lactase persistence example (i.e. Central Europe over the last 5000 years). Yet Simon and Coop find that this narrowly localized (at the genetic level) selective event, one of the strongest evidenced 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 change in genetic variation. Those patterns appear instead to be largely shaped by an influx of Yamnaya steppe pastoralists into Europe, and the genetic legacy of those migrants (Allentoft et al., 2024,1). But what allowed this influx to happen? What cultural traits allowed the Yamnaya to spread across Europe in the first place (e.g., technological innovations such as wagons, or a pervasive culture of horse riding that enabled their nomadic pastoralism, see (Anthony, 2023; Guyon et al., 2024; Karmin et al., 2015; Zeng et al., 2018))? Broad gene-culture coevolution sets out to explore such questions, and may attempt to link patterns of cultural change and heterogeneity 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 may necessarily miss many interesting phenomena.

2.2.1 Drift and gene-culture coevolution

Drift is a stochastic process of allele or trait frequency change that is fundamentally dependent on two factors: effective population sizes, and the strength of selection, if present. In finite populations, smaller population sizes magnify the effects of sampling errors which arise from gametic reproduction or stochastic between-individual variation in reproductive success. Additionally, as selection acts as a deterministic influence on allele frequency changes, its strength may limit the stochastic influence of drift (and vice versa). Both population size and strength of selection are likely to be profoundly shaped by culture (Shennan and Sear, 2020). Culture may intensify selection, 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 et al., 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 covary and jointly influence phenotypes, changes in cultural variation may mask genetic effects, effectively shielding the underlying genetic variation from selection and increasing the role of drift in determining the dynamics of genetic evolution (Cavalli-Sforza and Feldman, 1981; Durham, 1991; Laland and Brown, 2011; Uchiyama et al., 2021; Waring and Wood, 2021). Interestingly, as the relevant mechanism here still primarily concerns changes in selection coefficients, this particular aspect of drift-based gene-culture coevolution can be construed as covered by "narrow" gene-culture coevolution (e.g. Durham, 1991). In practice, however, investigating relaxed selection is not the usual aim of (empirical) gene-culture coevolutionary study.

Furthermore, the relative strength of random genetic drift (over selection) is also a function of the effective population size of reproducing individuals (Charlesworth, 2009; Hartl and Clark, 2007), which may also 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). Notably, drift may affect both genetic and cultural variation (Figure 2), because stochastic variation in transmission is likely also to influence cultural evolution: population size and other demographic factors, for example, likely play a role in the preservation of cultural variation and in the efficacy of cultural evolution to generate successful phenotypes (Cavalli-Sforza and Feldman, 1981; Deffner et al., 2022; Henrich, 2004; Strassberg and Creanza, 2020). Additionally, in a reversal of the cultural masking mechanism described above, genetically evolved traits that functionally overlap previously learned ones may release some cultural variation from selective constraints (e.g. via genetic assimilation, (Waddington, 1942,5); (Uchiyama et al., 2021)). In this way, a gene-culture coevolutionary theory of drift still encompasses a fundamentally reciprocal model of cultural and genetic evolution.

2.2.2 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 (Jablonski, 2004; McNamara et al., 2021; Yamaguchi and Hearing, 2009). Biologically, it is a function of the distribution of melanosomes in the skin, intracellular organelles generated by pigment cells, which synthesize 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 (Jablonski, 2021; Jablonski and Chaplin, 2010; Jones et al., 2018; Liu et al., 2024), claims 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 favored 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 favored in UVR-low environments (i.e. higher latitudes) to allow for more efficient photosynthesis of cutaneous Vitamin D (Jablonski, 2021; Loomis, 1967; Murray, 1934), generally thought to be a crucial nutrient in a wide of physiological processes (Lips, 2006,0), and which confers 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 emphasize 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 et al., 2007). Along a similar line of argument, Rifkin et al. (2015) hypothesize 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 in the diet. Culturally evolved subsistence practices modulate the dietary intake of Vitamin D, (de)emphasizing 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 may have exacerbated recent selection of depigmented skin (Marciniak and Perry, 2017; Richards et al., 2003; Wilde et al., 2014). 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 has been suggested 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 favoring 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 to explain phenotypic variation in skin coloration, including in Native American, European and Asian populations (Quillen et al., 2019). Further research in that regard could produce an 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.

2.2.3 Migration and gene-culture coevolution

Migration (or, in the genetic case, gene flow) is the other evolutionary mechanism that should be integrated 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 the whole globe (Cavalli-Sforza et al., 1996; Henn et al., 2012). The peopling of the world, now extensively traced through genomic as well as archeological 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 et al., 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, human migration, particularly in crossing 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 a deeply interconnected species. 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). This migratory tendency clearly affects both cultural variation (e.g. via demic or cultural diffusion) and its genetic counterpart (via gene flow and admixture). Demic and cultural diffusion are worth separating here, as cultural traits may "migrate" both in tandem with gene flow (via demic diffusion, i.e. the spread of holders of cultural traits, (Ammerman and Cavalli-Sforza, 1984)), or independently of it (via cultural diffusion, i.e. the spread of the cultural traits themselves through cultural transmission). Patterns of migration are likely deeply shaped by various eco-cultural forces influencing the modes, pathways and impetuses of migration - like navigational traditions modifying migratory reach (Bell, 2023; Kuhn et al., 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 (Cavalli-Sforza and Hewlett, 1982; Oota et al., 2001). Clearly, the role of culture in the dynamics of these processes is profound - yet its impact has largely been ignored in studies of gene-culture coevolution.

2.2.4 Example: Culture shapes the pathways of migration - Trade networks shape gene flow in Melanesia, and vice versa

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 Malinowski (1922) 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 painstakingly retraced 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 on 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 (Leach and Leach, 1983; Malinowski, 1922; Persson, 1983).

The functional and symbolic intricacies of the kula have received much attention over the decades following Malinowski's original description, and later anthropologists pointed 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 been reinforced across the region in a clear example of cultural transmission (Irwin et al., 2019). Additionally, the configuration and constancy of the kula ring were likely shaped by a 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 et al., 2019).

What might a gene-culture coevolutionary hypothesis for the kula look like, if gene flow were the primary mechanism of interest? 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 homogenization 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. A study by van Oven et al. (2014) examined patterns of paternally inherited Y-chromosomes (NRY) and maternally inherited mitochondrial DNA (mtDNA) across the Massim region. 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 emphasized by anthropologists). Two results stand out in evaluating the potential role of the kula in directing gene-flow in the region: First, 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; Seielstad et al., 1998), rendering post-marital residence norms an unlikely alternative explanation. Overall, van Oven et al. (2014) make a strong case for role of the kula in affecting the genetic structure of the Massim.

Subsequently, Liu et al. (2022) analyzed 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. They find 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 et al., 2019). They offer two non-exclusive explanations for the observed pattern: first, 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). Second, and particularly appealing to the reciprocal nature of coevolutionary approaches, Liu et al. (2022) speculate that it may, in part, have been the connectivity, shared ancestry and genealogical 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), as the resulting gift exchange network in turn may have facilitated gene flow that could reinforce those same kinship ties. This would serve as 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 differs from some other attempts at organizing 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 might be included in the gene–culture coevolutionary framework, this approach is more concerned with categorizing the respective targets (or levels) of reciprocal change, rather than the evolutionary mechanisms through which such targets interact. Therefore, it represents an approach that is orthogonal to our mechanism-focused taxonomy.

A classic attempt at categorizing gene-culture interactions comes from Durham (1991). In fact, Durham (1991) utilized a similar 'narrow' / 'broad' gene-culture coevolution terminology to that introduced here. However, Durham's approach does not include the role of what he calls "nonconveyance forces" in both genetic and cultural evolution, which include mutation, innovation, migration, and drift. Consequently, Durham's scheme 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) - leaving out "nonconveyance forces" entirely.

Following earlier research on whales suggesting that culture could shape neutral genetic variation and account for low genetic diversity (Whitehead, 2017), Whitehead et al. (2019) proposed a broader scheme of gene-culture coevolution that is roughly in line with our own. Like those authors, we propose that 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 roles that culture and cultural evolution play 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 possible 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). While we do extend the term beyond how it is typically used, we believe this concern to be equally valid in the case of gene-culture coevolution. A definition must be bounded, or it runs the risk of being diluted to the point of incoherence. For the purposes of clarity, it is therefore useful to reconsider some previous misgivings with the imprecise use of "coevolution" in evolutionary biology (Janzen, 1980). 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.

Specifically, one process that may lead to correspondence between genetic and cultural variation derives from the idiosyncrasies of a dual-inheritance system, and may help 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 each other'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 (Barbieri et al., 2022; Cavalli-Sforza et al., 1988; Penny et al., 1993; Sokal, 1988). These patterns might stem from parallel transmission of language and genes - via processes like "local codiffusion" (i.e. concurrent horizontal transmission) or simply be due to 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 each other's spread or dynamics, this does not constitute gene-culture coevolution.

Causal interaction through any 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 to be rather transient in human populations, possibly because language often evolves much faster than genes. Over longer time spans, as Barbieri et al. (2022) point out, linguistic and genetic lineages may give different estimates of divergence times, leading the authors to assert that instead, preceding genetic diversification may trigger later cultural diversification, whereas early linguistic diversification may cause barriers to gene flow which affect genetic structure. Both of these scenarios, in turn, would be coevolutionary mechanisms that satisfy our simple criterion of non-independent co-inheritance. Another interesting case is that of gene-culture hitchhiking, where parallel transmission of genetic and cultural variation leads to incidental linkage between the two, so that subsequent selection in one domain leads to reduction in variation in the other (Zeng et al., 2018). Here, although genes and culture do not interact directly, their association may lead to coevolutionary dynamics. Nevertheless, perfect parallel transmission without linked selection should serve as a useful null model for empirical investigations of gene-culture coevolution where correspondences between genetic and cultural variation are observed. 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).

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, even supportive of, gene-culture coevolution as a theoretical framework. This work, despite not being explicitly framed as gene-culture coevolution, perhaps partly 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 (Balanovsky et al., 2011; Barbujani and Sokal, 1990; Pichkar and Creanza, 2023), post-marital residence norms (Cavalli-Sforza and Hewlett, 1982; Oota et al., 2001; Seielstad et al., 1998), subsistence transitions (Padilla-Iglesias and Derkx, 2024), assortative mating (Robinson et al., 2017; Yengo et al., 2018), culturally-determined social stratification (Basu et al., 2016; Moorjani et al., 2013), or endogamy and consanguineous marriage norms (Bittles and Black, 2010).

Looking to the future, we hope that our framework may open new avenues of theoretically motivated empirical

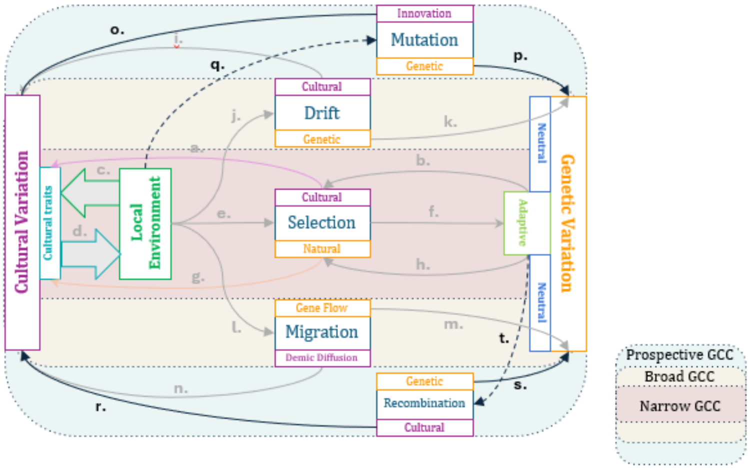

Figure 3: **Potential areas of future research on gene-culture interactions.** Conceivably, there are gene-culture coevolutionary processes beyond those outlined in previous figures, concerned with additional candidate mechanisms that we have sidelined. Some plausible causal links, suggested from adjacent 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 favoring 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 et al., 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).

research on gene-culture coevolution. By using a broader range of well-established evolutionary mechanisms or forces as the organizing principle for understanding gene-culture interactions, broad gene-culture coevolution may provide a promising and simple way of detecting novel 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 lead to 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 care required by their respective complexities. The vision of gene-culture coevolution laid out here is, fundamentally, interdisciplinary: 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 exploring the 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 promote 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, guiding framework, the constituent parts of which can be investigated using any number of approaches. This includes human behavioral ecology (e.g. examining the relationship between cultural traditions and ecology; (Micheletti et al., 2023)), psychology (examining how cross-cultural cognition and the cognitive machinery of social learning emerge in the first place; (Mesoudi, 2009)), and cultural evolution itself. Other recent work has similarly argued for some conceptual rearrangement and synthesis (Micheletti et al., 2022,2).

We are not proposing a final, all-encompassing 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 be, and have been, construed to be evolutionary processes - most notably mutation, but also recombination or assortative mating (e.g., Mayr, 2002; Posada et al., 2002). It is conceivable, even likely, that cultural influences may play a role in those domains as well. For example, given the well-established role of parental age on the human germline mutation rate (Gao et al., 2019; Girard et al., 2016), it is possible that 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).

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 with which we share environments and ecosystem, including both animal and plant domesticates (Hendry et al., 2017). Staying with gene-culture coevolution's flagship example, new evidence suggests for instance that lactase persistence alleles have also been selected for in European dogs (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 et al., 2012). This doubtlessly opens many avenues for scientific inquiry, including how the spread of certain cultural traits may correspond to the genetic structure of many domesticated organisms. The same goes for considerations of gene-culture coevolution beyond the human domain: The study of 'animal cultures', socially acquired behavioral traditions in non-human animals, is a growing science (Laland and Hoppitt, 2003; Schuppli and van Schaik, 2019; Whiten, 2021). There is now rapidly accumulating evidence that the same interactions that mark human cultural and genetic evolution may lead to gene-culture coevolutionary phenomena in non-human animals (Whitehead et al., 2019), spanning the animal kingdom from cetaceans to insects (Bridges and Chittka, 2019; Whitehead, 2017). The applicability of a gene-culture coevolution framework outside of human evolution should help to integrate the theory into 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 encourage a more inclusive analysis of the potential causal interactions between genes and culture. Empirical investigation of gene-culture coevolution remains a fledgling scientific effort, but our hope is that expanding the rigorous theoretical framework in which gene-culture coevolution was originally conceived may prove to be useful 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). Ultimately, it will surely take a concerted, cross-disciplinary effort to answer this one simple question: how, and to what extent, have humans shaped their own evolution?

References

Allentoft, M. E., Sikora, M., Refoyo-Martínez, A., Irving-Pease, E. K., Fischer, A., Barrie, W., Ingason, A., Stenderup, J., Sjögren, K.-G., Pearson, A., Sousa da Mota, B., Schulz Paulsson, B., Halgren, A., Macleod, R., Jørkov, M. L. S., Demeter, F., Sørensen, L., Nielsen, P. O., Henriksen, R. A., Vimala, T., McColl, H., Margaryan, A., Ilardo, M., Vaughn, A., Fischer Mortensen, M., Nielsen, A. B., Ulfeldt Hede, M., Johannsen, N. N., Rasmussen, P., Vinner, L., Renaud, G., Stern, A., Jensen, T. Z. T., Scorrano, G., Schroeder, H., Lysdahl, P., Ramsøe, A. D., Skorobogatov, A., Schork, A. J., Rosengren, A., Ruter, A., Outram, A., Timoshenko, A. A., Buzhilova, A., Coppa, A., Zubova, A., Silva, A. M., Hansen, A. J., Gromov, A., Logvin, A., Gotfredsen, A. B., Henning Nielsen, B., González-Rabanal, B., Lalueza-Fox, C., McKenzie, C. J., Gaunitz, C., Blasco, C., Liesau, C., Martinez-Labarga, C., Pozdnyakov, D. V., Cuenca-Solana, D., Lordkipanidze, D. O., En'shin, D., Salazar-García, D. C., Price, T. D., Borić, D., Kostyleva, E., Veselovskaya, E. V., Usmanova, E. R., Cappellini, E., Brinch Petersen, E., Kannegaard, E., Radina, F., Eylem Yediay, F., Duday, H., Gutiérrez-Zugasti, I., Merts, I., Potekhina, I., Shevnina, I., Altinkaya, I., Guilaine, J., Hansen, J., Aura Tortosa, J. E., Zilhão, J., Vega, J., Buck Pedersen, K., Tunia, K., Zhao, L., Mylnikova, L. N., Larsson, L., Metz, L., Yepiskoposyan, L., Pedersen, L., Sarti, L., Orlando, L., Slimak, L., Klassen, L., Blank, M., González-Morales, M., Silvestrini, M., Vretemark, M., Nesterova, M. S., Rykun, M., Rolfo, M. F., Szmyt, M., Przybyła, M., Calattini, M., Sablin, M., Dobisíková, M., Meldgaard, M., Johansen, M., Berezina, N., Card, N., Saveliev, N. A., Poshekhonova, O., Rickards, O., Lozovskaya, O. V., Gábor, O., Uldum, O. C., Aurino, P., Kosintsev, P., Courtaud, P., Ríos, P., Mortensen, P., Lotz, P., Persson, P., Bangsgaard, P., de Barros Damgaard, P., Vang Petersen, P., Martinez, P. P., Włodarczak, P., Smolyaninov, R. V., Maring, R., Menduiña, R., Badalyan, R., Iversen, R., Turin, R., Vasilyev, S., Wåhlin, S., Borutskaya, S., Skochina, S., Sørensen, S. A., Andersen, S. H., Jørgensen, T., Serikov, Y. B., Molodin, V. I., Smrcka, V., Merts, V., Appadurai, V., Moiseyev, V., Magnusson, Y., Kjær, K. H., Lynnerup, N., Lawson, D. J., Sudmant, P. H., Rasmussen, S., Korneliussen, T. S., Durbin, R., Nielsen, R., Delaneau, O., Werge, T., Racimo, F., Kristiansen, K., and Willerslev, E. (2024). Population genomics of post-glacial western Eurasia. *Nature*, 625(7994):301–311.

Allentoft, M. E., Sikora, M., Sjögren, K.-G., Rasmussen, S., Rasmussen, M., Stenderup, J., Damgaard, P. B., Schroeder, H., Ahlström, T., Vinner, L., Malaspinas, A.-S., Margaryan, A., Higham, T., Chivall, D., Lynnerup, N., Harvig, L., Baron, J., Casa, P. D., Dabrowski, P., Duffy, P. R., Ebel,

A. V., Epimakhov, A., Frei, K., Furmanek, M., Gralak, T., Gromov, A., Gronkiewicz, S., Grupe, G., Hajdu, T., Jarysz, R., Khartanovich, V., Khokhlov, A., Kiss, V., Kolář, J., Kriiska, A., Lasak, I., Longhi, C., McGlynn, G., Merkevicius, A., Merkyte, I., Metspalu, M., Mkrtchyan, R., Moiseyev, V., Paja, L., Pálfi, G., Pokutta, D., Pospieszny, Ł., Price, T. D., Saag, L., Sablin, M., Shishlina, N., Smrčka, V., Soenov, V. I., Szeverényi, V., Tóth, G., Trifanova, S. V., Varul, L., Vicze, M., Yepiskoposyan, L., Zhitenev, V., Orlando, L., Sicheritz-Pontén, T., Brunak, S., Nielsen, R., Kristiansen, K., and Willerslev, E. (2015). Population genomics of bronze age eurasia. *Nature*, 522(7555):167–172.

Ammerman, A. J. and Cavalli-Sforza, L. L. (1984). *The Neolithic Transition and the Genetics of Populations in Europe.* Princeton University Press.

Anderson, A. (2008). Traditionalism, interaction, and long-distance seafaring in polynesia. *The Journal of Island and Coastal Archaeology*, 3(2):240–250.

Anthony, D. W. (2023). The yamnaya culture and the invention of nomadic pastoralism in the eurasian steppes. In Kristiansen, K., Kroonen, G., and Willerslev, E., editors, *The Indo-European Puzzle Revisited: Integrating Archaeology, Genetics, and Linguistics*, page 13–33. Cambridge University Press.

Aoki, K. (1986). A stochastic model of gene-culture coevolution suggested by the ”culture historical hypothesis” for the evolution of adult lactose absorption in humans. *Proceedings of the National Academy of Sciences*, 83(9):2929–2933.

Aoki, K. (2001). Theoretical and empirical aspects of gene–culture coevolution. *Theoretical Population Biology*, 59(4):253–261.

Balanovsky, O., Dibirova, K., Dybo, A., Mudrak, O., Frolova, S., Pocheshkhova, E., Haber, M., Platt, D., Schurr, T., Haak, W., Kuznetsova, M., Radzhabov, M., Balaganskaya, O., Romanov, A., Zakharova, T., Soria Hernanz, D. F., Zalloua, P., Koshel, S., Ruhlen, M., Renfrew, C., Wells, R. S., Tyler-Smith, C., Balanovska, E., and The Genographic Consortium (2011). Parallel evolution of genes and languages in the caucasus region. *Molecular Biology and Evolution*, 28(10):2905–2920.

Barbieri, C., Blasi, D. E., Arango-Isaza, E., Sotiropoulos, A. G., Hammarström, H., Wichmann, S., Greenhill, S. J., Gray, R. D., Forkel, R., Bickel, B., and Shimizu, K. K. (2022). A global analysis of matches and mismatches between human genetic and linguistic histories. *Proceedings of the National Academy of Sciences*, 119(47):e2122084119.

Barbujani, G. and Sokal, R. R. (1990). Zones of sharp genetic change in Europe are also linguistic boundaries. *Proceedings of the National Academy of Sciences*, 87(5):1816–1819.

Basu, A., Sarkar-Roy, N., and Majumder, P. P. (2016). Genomic reconstruction of the history of extant populations of India reveals five distinct ancestral components and a complex structure. *Proceedings of the National Academy of Sciences*, 113(6):1594–1599.

Bell, A. V. (2023). Selection and adaptation in human migration. *Evolutionary Anthropology: Issues,* *News, and Reviews*, 32(6):308–324.

Bittles, A. and Black, M. (2010). Consanguineous marriage and human evolution. *Annual Review of Anthropology*, 39(1):193–207.

Bolognini, D., Halgren, A., Lou, R. N., Raveane, A., Rocha, J. L., Guarracino, A., Soranzo, N., Chin, C.-S., Garrison, E., and Sudmant, P. H. (2024). Recurrent evolution and selection shape structural diversity at the amylase locus. *Nature*, 634(8034):617–625.

Boyd, R. and Richerson, P. J. (1985). *Culture and the Evolutionary Process*. University of Chicago Press, Chicago.

Branda, R. F. and Eaton, J. W. (1978). Skin color and nutrient photolysis: An evolutionary hypothesis. *Science*, 201(4356):625–626.

Bridges, A. D. and Chittka, L. (2019). Animal behaviour: Conformity and the beginnings of culture in an insect. *Current Biology*, 29(5):R167–R169.

Cai, J. J., Macpherson, J. M., Sella, G., and Petrov, D. A. (2009). Pervasive hitchhiking at coding and regulatory sites in humans. *PLOS Genetics*, 5(1):e1000336.

Campbell, M. C. and Ranciaro, A. (2021). Human adaptation, demography and cattle domestication: An overview of the complexity of lactase persistence in Africa. *Human Molecular Genetics*, 30(R1):R98–R109.

Cavalli-Sforza, L. L. and Feldman, M. W. (1973). Cultural versus biological inheritance: Phenotypic transmission from parents to children. (A theory of the effect of parental phenotypes on children's phenotypes). *American Journal of Human Genetics*, 25(6):618–637.

Cavalli-Sforza, L. L. and Feldman, M. W. (1981). *Cultural Transmission and Evolution : A Quantitative Approach*. Monographs in Population Biology. Princeton University Press, Princeton, N.J.

Cavalli-Sforza, L. L. and Hewlett, B. (1982). Exploration and mating range in African Pygmies. *Annals of Human Genetics*, 46(3):257–270.

Cavalli-Sforza, L. L., Menozzi, P., and Piazza, A. (1996). *The History and Geography of Human Genes: Abridged Paperback Edition*. Princeton University Press.

Cavalli-Sforza, L. L., Piazza, A., Menozzi, P., and Mountain, J. (1988). Reconstruction of human evolution: Bringing together genetic, archaeological, and linguistic data. *Proceedings of the National Academy of Sciences*, 85(16):6002–6006.

Charlesworth, B. (2009). Effective population size and patterns of molecular evolution and variation. *Nature Reviews Genetics*, 10(3):195–205.

Chudek, M. and Henrich, J. P. (2011). Culture–gene coevolution, norm-psychology and the emergence of human prosociality. *Trends in Cognitive Sciences*, 15(5):218–226.

Conner, J. K. (2003). Artificial selection: A powerful tool for ecologists. *Ecology*, 84(7):1650–1660.

Creanza, N., Kolodny, O., and Feldman, M. W. (2017). Greater than the sum of its parts? Modelling population contact and interaction of cultural repertoires. *Journal of The Royal Society Interface*, 14(130):20170171.

Day, R. L., Laland, K. N., and Odling-Smee, F. J. (2003). Rethinking adaptation: The niche-construction perspective. *Perspectives in biology and medicine*, 46(1):80–95.

Deffner, D., Kandler, A., and Fogarty, L. (2022). Effective population size for culturally evolving traits. *PLOS Computational Biology*, 18(4):e1009430.

Denton, K. K., Kendal, J. R., Ihara, Y., and Feldman, M. W. (2023). Cultural niche construction with application to fertility control: A model for education and social transmission of contraceptive use. *Theoretical Population Biology*, 153:1–14.

Deutch, B., Dyerberg, J., Pedersen, H. S., Aschlund, E., and Hansen, J. C. (2007). Traditional and modern Greenlandic food — Dietary composition, nutrients and contaminants. *Science of The Total Environment*, 384(1):106–119.

Durham, W. H. (1991). *Coevolution: Genes, Culture, and Human Diversity.* Stanford University Press, Stanford.

Evershed, R. P., Davey Smith, G., Roffet-Salque, M., Timpson, A., Diekmann, Y., Lyon, M. S., Cramp, L. J. E., Casanova, E., Smyth, J., Whelton, H. L., Dunne, J., Brychova, V., Šoberl, L., Gerbault, P., Gillis, R. E., Heyd, V., Johnson, E., Kendall, I., Manning, K., Marciniak, A., Outram, A. K., Vigne, J.-D., Shennan, S., Bevan, A., Colledge, S., Allason-Jones, L., Amkreutz, L., Anders, A., Arbogast, R.-M., Bălăşescu, A., Bánffy, E., Barclay, A., Behrens, A., Bogucki, P., Carrancho Alonso, Á., Carretero, J. M., Cavanagh, N., Claßen, E., Collado Giraldo, H., Conrad, M., Csengeri, P., Czerniak, L., Debiec, M., Denaire, A., Domboróczki, L., Donald, C., Ebert, J., Evans, C., Francés-Negro, M., Gronenborn, D., Haack, F., Halle, M., Hamon, C., Hülshoff, R., Ilett, M., Iriarte, E., Jakucs, J., Jeunesse, C., Johnson, M., Jones, A. M., Karul, N., Kiosak, D., Kotova, N., Krause, R., Kretschmer, S., Krüger, M., Lefranc, P., Lelong, O., Lenneis, E., Logvin, A., Lüth, F., Marton, T., Marley, J., Mortimer, R., Oosterbeek, L., Oross, K., Pavúk, J., Pechtl, J., Pétrequin, P., Pollard, J., Pollard, R., Powlesland, D., Pyzel, J., Raczky, P., Richardson, A., Rowe, P., Rowland, S., Rowlandson, I., Saile, T., Sebők, K., Schier, W., Schmalfuß, G., Sharapova, S., Sharp, H., Sheridan, A., Shevnina, I., Sobkowiak-Tabaka, I., Stadler, P., Stäuble, H., Stobbe, A., Stojanovski, D., Tasić, N., van Wijk, I., Vostrovská, I., Vuković, J., Wolfram, S., Zeeb-Lanz, A., and Thomas, M. G. (2022). Dairying, diseases and the evolution of lactase persistence in Europe. *Nature*, 608(7922):336–345.

Feldman, M. W. and Cavalli-Sforza, L. L. (1984). Cultural and biological evolutionary processes: Gene-culture disequilibrium. *Proceedings of the National Academy of Sciences*, 81(5):1604–1607.

Feldman, M. W. and Cavalli-Sforza, L. L. (1989). 8. on the theory of evolution under genetic and cultural transmission, with application to the lactose absorption problem. In *Mathematical Evolutionary Theory*, pages 139–173. Princeton University Press, Princeton.

Feldman, M. W. and Laland, K. N. (1996). Gene-culture coevolutionary theory. *Trends in Ecology & Evolution*, 11(11):453–457.

Feldman, M. W. and Ramachandran, S. (2018). Missing compared to what? Revisiting heritability, genes and culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1743):20170064.

Fernandez-Velasco, P. and Spiers, H. J. (2024). Wayfinding across ocean and tundra: What traditional cultures teach us about navigation. *Trends in Cognitive Sciences*, 28(1):56–71.

Fumagalli, M., Moltke, I., Grarup, N., Racimo, F., Bjerregaard, P., Jørgensen, M. E., Korneliussen, T. S., Gerbault, P., Skotte, L., Linneberg, A., Christensen, C., Brandslund, I., Jørgensen, T., Huerta-Sánchez, E., Schmidt, E. B., Pedersen, O., Hansen, T., Albrechtsen, A., and Nielsen, R. (2015). Greenlandic Inuit show genetic signatures of diet and climate adaptation. *Science*, 349(6254):1343–1347.

Gao, Z., Moorjani, P., Sasani, T. A., Pedersen, B. S., Quinlan, A. R., Jorde, L. B., Amster, G., and Przeworski, M. (2019). Overlooked roles of DNA damage and maternal age in generating human germline mutations. *Proceedings of the National Academy of Sciences*, 116(19):9491–9500.

Gao, Z., Zhang, Y., Cramer, N., Przeworski, M., and Moorjani, P. (2023). Limited role of generation time changes in driving the evolution of the mutation spectrum in humans. *eLife*, 12:e81188.

Gerbault, P., Liebert, A., Itan, Y., Powell, A., Currat, M., Burger, J., Swallow, D. M., and Thomas, M. G. (2011). Evolution of lactase persistence: An example of human niche construction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1566):863–877.

Gintis, H. (2011). Gene–culture coevolution and the nature of human sociality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1566):878–888.

Girard, S. L., Bourassa, C. V., Perreault, L.-P. L., Legault, M.-A., Barhdadi, A., Ambalavanan, A., Brendgen, M., Vitaro, F., Noreau, A., Dionne, G., Tremblay, R. E., Dion, P. A., Boivin, M., Dubé, M.-P., and Rouleau, G. A. (2016). Paternal age explains a major portion of de novo germline mutation rate variability in healthy individuals. *PLOS ONE*, 11(10):e0164212.

Guyon, L., Guez, J., Toupance, B., Heyer, E., and Chaix, R. (2024). Patrilineal segmentary systems provide a peaceful explanation for the post-Neolithic Y-chromosome bottleneck. *Nature Communications*, 15(1):3243.

Han, Y., Gu, S., Oota, H., Osier, M. V., Pakstis, A. J., Speed, W. C., Kidd, J. R., and Kidd, K. K. (2007). Evidence of positive selection on a class I ADH locus. *The American Journal of Human Genetics*, 80(3):441–456.

Hartl, D. L. and Clark, A. G. (2007). *Principles of Population Genetics*. Sinauer Associates, Sunderland, Mass., 4 edition.

Heath, K. M., Axton, J. H., McCullough, J. M., and Harris, N. (2016). The evolutionary adaptation of the C282Y mutation to culture and climate during the European Neolithic. *American Journal of Physical Anthropology*, 160(1):86–101.

Hellmann, I., Mang, Y., Gu, Z., Li, P., de la Vega, F. M., Clark, A. G., and Nielsen, R. (2008). Population genetic analysis of shotgun assemblies of genomic sequences from multiple individuals. *Genome Research*, 18(7):1020–1029.

Hendry, A. P., Gotanda, K. M., and Svensson, E. I. (2017). Human influences on evolution, and the ecological and societal consequences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1712):20160028.

Henn, B. M., Cavalli-Sforza, L. L., and Feldman, M. W. (2012). The great human expansion. *Proceedings of the National Academy of Sciences*, 109(44):17758–17764.

Henrich, J. P. (2004). Demography and cultural evolution: How adaptive cultural processes can produce maladaptive losses—the tasmanian case. *American Antiquity*, 69(2):197–214.

Henrich, J. P. (2015). *The Secret of Our Success : How Culture Is Driving Human Evolution, Domesticating Our Species, and Making Us Smarter*. Princeton University Press, Princeton.

Holden, C. and Mace, R. (1997). Phylogenetic analysis of the evolution of lactose digestion in adults. *Human Biology*, 69(5):605–628.

Holick, M. F. (2006). Resurrection of vitamin D deficiency and rickets. *The Journal of Clinical Investigation*, 116(8):2062–2072.

Hughes, D. A., Tang, K., Strotmann, R., Schöneberg, T., Prenen, J., Nilius, B., and Stoneking, M. (2008). Parallel selection on TRPV6 in human populations. *PLOS ONE*, 3(2):e1686.

Hunter, D. J. (2005). Gene–environment interactions in human diseases. *Nature Reviews Genetics*, 6(4):287–298.

Ihara, Y. and W. Feldman, M. (2004). Cultural niche construction and the evolution of small family size. *Theoretical Population Biology*, 65(1):105–111.

Ingram, C. J. E., Raga, T. O., Tarekegn, A., Browning, S. L., Elamin, M. F., Bekele, E., Thomas, M. G., Weale, M. E., Bradman, N., and Swallow, D. M. (2009). Multiple rare variants as a cause of a common phenotype: Several different lactase persistence associated alleles in a single ethnic group. *Journal of Molecular Evolution*, 69(6):579.

Irwin, G., Shaw, B., and Mcalister, A. (2019). The origins of the kula ring: Archaeological and maritime perspectives from the southern massim and mailu areas of papua new guinea. *Archaeology in Oceania*, 54(1):1–16.

Jablonski, N. G. (2004). The evolution of human skin and skin color. *Annual Review of Anthropology*, 33(1):585–623.

Jablonski, N. G. (2021). The evolution of human skin pigmentation involved the interactions of genetic, environmental, and cultural variables. *Pigment Cell & Melanoma Research*, 34(4):707–729.

Jablonski, N. G. and Chaplin, G. (2010). Human skin pigmentation as an adaptation to UV radiation. *Proceedings of the National Academy of Sciences*, 107(supplement_2):8962–8968.

Janzen, D. H. (1980). When is it coevolution? *Evolution; international journal of organic evolution*, 34(3):611–612.

Jones, P., Lucock, M., Veysey, M., and Beckett, E. (2018). The vitamin d–folate hypothesis as an evolutionary model for skin pigmentation: An update and integration of current ideas. *Nutrients*, 10(5):554.

Jordan, F. M., Gray, R. D., Greenhill, S. J., and Mace, R. (2009). Matrilocal residence is ancestral in Austronesian societies. *Proceedings of the Royal Society B: Biological Sciences*, 276(1664):1957–1964.

Karmin, M., Saag, L., Vicente, M., Sayres, M. A. W., Järve, M., Talas, U. G., Rootsi, S., Ilumäe, A.-M., Mägi, R., Mitt, M., Pagani, L., Puurand, T., Faltyskova, Z., Clemente, F., Cardona, A., Metspalu, E., Sahakyan, H., Yunusbayev, B., Hudjashov, G., DeGiorgio, M., Loogväli, E.-L., Eichstaedt, C., Eelmets, M., Chaubey, G., Tambets, K., Litvinov, S., Mormina, M., Xue, Y., Ayub, Q., Zoraqi, G., Korneliussen, T. S., Akhatova, F., Lachance, J., Tishkoff, S., Momynaliev, K., Ricaut, F.-X., Kusuma, P., Razafindrazaka, H., Pierron, D., Cox, M. P., Sultana, G. N. N., Willerslev, R., Muller, C., Westaway, M., Lambert, D., Skaro, V., Kovačevic´, L., Turdikulova, S., Dalimova, D., Khusainova, R., Trofimova, N., Akhmetova, V., Khidiyatova, I., Lichman, D. V., Isakova, J., Pocheshkhova, E., Sabitov, Z., Barashkov, N. A., Nymadawa, P., Mihailov, E., Seng, J. W. T., Evseeva, I., Migliano, A. B., Abdullah, S., Andriadze, G., Primorac, D., Atramentova, L., Utevska, O., Yepiskoposyan, L., Marjanovic´, D., Kushniarevich, A., Behar, D. M., Gilissen, C., Vissers, L., Veltman, J. A., Balanovska, E., Derenko, M., Malyarchuk, B., Metspalu, A., Fedorova, S., Eriksson, A., Manica, A., Mendez, F. L., Karafet, T. M., Veeramah, K. R., Bradman, N., Hammer, M. F., Osipova, L. P., Balanovsky, O., Khusnutdinova, E. K., Johnsen, K., Remm, M., Thomas, M. G., Tyler-Smith, C., Underhill, P. A., Willerslev, E., Nielsen, R., Metspalu, M., Villems, R., and Kivisild, T. (2015). A recent bottleneck of Y chromosome diversity coincides with a global change in culture. *Genome Research*, 25(4):459–466.

Kendal, J. R. (2015). Gene–culture coevolution. In Wright, J. D., editor, *International Encyclopedia of the Social & Behavioral Sciences*, pages 813–818. Elsevier, Oxford.

Kendal, J. R., Tehrani, J. J., and Odling-Smee, J. (2011). Human niche construction in interdisciplinary focus. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1566):785–792.

Kendal, R. L., Boogert, N. J., Rendell, L., Laland, K. N., Webster, M., and Jones, P. L. (2018). Social learning strategies: Bridge-building between fields. *Trends in Cognitive Sciences*, 22(7):651–665.

Kuhn, S. L., Raichlen, D. A., and Clark, A. E. (2016). What moves us? How mobility and movement are at the center of human evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, 25(3):86–97.

Laland, K. N. (2017). *Darwin's Unfinished Symphony.* Princeton University Press.

Laland, K. N. and Brown, G. R. (2011). *Sense and Nonsense : Evolutionary Perspectives on Human Behaviour.* Oxford University Press, Oxford, 2 edition.

Laland, K. N. and Hoppitt, W. (2003). Do animals have culture? *Evolutionary Anthropology: Issues, News, and Reviews*, 12(3):150–159.

Laland, K. N., Odling-Smee, F. J., and Feldman, M. W. (2001). Cultural niche construction and human evolution. *Journal of Evolutionary Biology*, 14(1):22–33.

Lamberg-Allardt, C. (2006). Vitamin D in foods and as supplements. *Progress in Biophysics and Molecular Biology*, 92(1):33–38.

Lautenschlager, S., Wulf, H. C., and Pittelkow, M. R. (2007). Photoprotection. *The Lancet*, 370(9586):528–537.

Leach, J. W. and Leach, E. (1983). *The Kula: New Perspectives on Massim Exchange.* CUP Archive.

Lewinsky, R. H., Jensen, T. G. K., Møller, J., Stensballe, A., Olsen, J., and Troelsen, J. T. (2005). T-13910 DNA variant associated with lactase persistence interacts with Oct-1 and stimulates lactase promoter activity in vitro. *Human Molecular Genetics*, 14(24):3945–3953.

Lewontin, R. C. (1989). Gene, organism, and environment. In Bendall, D. S., editor, *Evolution from Molecules to Men*, pages 273–286. Cambridge University Press, Cambridge, UK.

Lin, J. Y. and Fisher, D. E. (2007). Melanocyte biology and skin pigmentation. *Nature*, 445(7130):843–850.

Lips, P. (2006). Vitamin D physiology. *Progress in Biophysics and Molecular Biology*, 92(1):4–8.

Lips, P. (2007). Vitamin D status and nutrition in europe and asia. *The Journal of Steroid Biochemistry and Molecular Biology*, 103(3):620–625.

Liu, D., Peter, B. M., Schiefenhövel, W., Kayser, M., and Stoneking, M. (2022). Assessing human genome-wide variation in the massim region of papua new guinea and implications for the kula trading tradition. *Molecular Biology and Evolution*, 39(8):msac165.

Liu, J., Bitsue, H. K., and Yang, Z. (2024). Skin colour: A window into human phenotypic evolution and environmental adaptation. *Molecular Ecology*, n/a(n/a):e17369.

Liu, Y.-H., Wang, L., Zhang, Z., Otecko, N. O., Khederzadeh, S., Dai, Y., Liang, B., Wang, G.-D., and Zhang, Y.-P. (2021). Whole-genome sequencing reveals lactase persistence adaptation in european dogs. *Molecular Biology and Evolution*, 38(11):4884–4890.

Loomis, W. F. (1967). Skin-pigment regulation of vitamin-d biosynthesis in man. *Science*, 157(3788):501–506.

Macpherson, J. M., Ramachandran, S., Diamond, L., and Feldman, M. W. (2004). Demographic estimates from Y chromosome microsatellite polymorphisms: Analysis of a worldwide sample. *Human*

Genomics, 1(5):345.

Malinowski, B. (1922). Argonauts of the western pacific: An account of native enterprise and adventure in the archipelagoes of melanesian new guinea. *Studies in economics and political science (*, (65).

Manuck, S. B. and McCaffery, J. M. (2014). Gene-environment interaction. *Annual Review of Psychology*, 65(1):41–70.

Marciniak, S. and Perry, G. H. (2017). Harnessing ancient genomes to study the history of human adaptation. *Nature Reviews Genetics*, 18(11):659–674.

Mathew, S. and Perreault, C. (2015). Behavioural variation in 172 small-scale societies indicates that social learning is the main mode of human adaptation. *Proceedings of the Royal Society B: Biological Sciences*, 282(1810):20150061.

Mayr, E. (2002). *What Evolution Is*. Science Masters. Weidenfeld & Nicolson, London.

McCracken, R. D. (1971). Lactase deficiency: An example of dietary evolution. *Current Anthropology*, 12(4/5):479–517.

McGue, M. and Bouchard, T. J. (1998). Genetic and environmental influences on human behavioral differences. *Annual Review of Neuroscience*, 21(1):1–24.

McNamara, M. E., Rossi, V., Slater, T. S., Rogers, C. S., Ducrest, A. L., Dubey, S., and Roulin, A. (2021). Decoding the evolution of melanin in vertebrates. *Trends in Ecology & Evolution*, 36(5):430–443.

McVicker, G., Gordon, D., Davis, C., and Green, P. (2009). Widespread genomic signatures of natural selection in hominid evolution. *PLOS Genetics*, 5(5):e1000471.

Mesoudi, A. (2009). How cultural evolutionary theory can inform social psychology and vice versa. *Psychological Review*, 116(4):929–952.

Mesoudi, A. (2011). *Cultural Evolution: How Darwinian Theory Can Explain Human Culture and Synthesize the Social Sciences*. University of Chicago Press, Chicago ; London.

Meyer, R. S., DuVal, A. E., and Jensen, H. R. (2012). Patterns and processes in crop domestication: An historical review and quantitative analysis of 203 global food crops. *New Phytologist*, 196(1):29–48.

Micheletti, A. J. C., Brandl, E., and Mace, R. (2022). What is cultural evolution anyway? *Behavioral Ecology*, 33(4):667–669.

Micheletti, A. J. C., Brandl, E., Zhang, H., Peacey, S., and Mace, R. (2023). Cultural evolution research needs to include human behavioural ecology. In du Crest, A., Valković, M., Ariew, A., Desmond, H., Huneman, P., and Reydon, T. A. C., editors, *Evolutionary Thinking Across Disciplines: Problems and Perspectives in Generalized Darwinism*, pages 501–528. Springer International Publishing, Cham.

Moorjani, P., Thangaraj, K., Patterson, N., Lipson, M., Loh, P.-R., Govindaraj, P., Berger, B., Reich, D., and Singh, L. (2013). Genetic evidence for recent population mixture in india. *The American Journal of Human Genetics*, 93(3):422–438.

Murphy, D. A., Elyashiv, E., Amster, G., and Sella, G. (2022). Broad-scale variation in human genetic diversity levels is predicted by purifying selection on coding and non-coding elements. *eLife*, 12:e76065.

Murray, F. G. (1934). Pigmentation, sunlight, and nutritional disease. *American Anthropologist*, 36(3):438–445.

Nielsen, R., Akey, J. M., Jakobsson, M., Pritchard, J. K., Tishkoff, S., and Willerslev, E. (2017). Tracing the peopling of the world through genomics. *Nature*, 541(7637):302–310.

Nisbett, R. E., Aronson, J., Blair, C., Dickens, W., Flynn, J., Halpern, D. F., and Turkheimer, E. (2012). Intelligence: New findings and theoretical developments. *American Psychologist*, 67(2):130–159.

O'Brien, M. J. and Laland, K. N. (2012). Genes, culture, and agriculture: An example of human niche construction. *Current Anthropology*, 53(4):434–470.

Oota, H., Settheetham-Ishida, W., Tiwawech, D., Ishida, T., and Stoneking, M. (2001). Human mtDNA and Y-chromosome variation is correlated with matrilocal versus patrilocal residence. *Nature Genetics*, 29(1):20–21.

Osier, M. V., Pakstis, A. J., Soodyall, H., Comas, D., Goldman, D., Odunsi, A., Okonofua, F., Parnas, J., Schulz, L. O., Bertranpetit, J., Bonne-Tamir, B., Lu, R.-B., Kidd, J. R., and Kidd, K. K. (2002). A global perspective on genetic variation at the ADH genes reveals unusual patterns of linkage disequilibrium and diversity. *The American Journal of Human Genetics*, 71(1):84–99.

Padilla-Iglesias, C. and Derkx, I. (2024). Hunter–gatherer genetics research: Importance and avenues. *Evolutionary Human Sciences*, 6:e15.

Pearl, J. (2009). Causal inference in statistics: An overview. *Statistics Surveys*, 3(none):96–146.

Peng, Y., Shi, H., Qi, X.-b., Xiao, C.-j., Zhong, H., Ma, R.-l. Z., and Su, B. (2010). The ADH1B Arg47His polymorphism in East Asian populations and expansion of rice domestication in history. *BMC Evolutionary Biology*, 10(1):15.

Penny, D., Watson, E. E., and Steel, M. A. (1993). Trees from languages and genes are very similar. *Systematic Biology*, 42(3):382–384.

Perry, G. H., Dominy, N. J., Claw, K. G., Lee, A. S., Fiegler, H., Redon, R., Werner, J., Villanea, F. A., Mountain, J. L., Misra, R., Carter, N. P., Lee, C., and Stone, A. C. (2007). Diet and the evolution of human amylase gene copy number variation. *Nature Genetics*, 39(10):1256–1260.

Persson, J. (1983). Cyclical change and circular exchange: A re-examination of the KULA ring. *Oceania; a journal devoted to the study of the native peoples of Australia, New Guinea, and the Islands of the Pacific*, 54(1):32–47.

Pichkar, Y. and Creanza, N. (2023). Fine-scale cultural variation reinforces genetic structure in England. *American Journal of Biological Anthropology*, 181(4):626–636.

Posada, D., Crandall, K. A., and Holmes, E. C. (2002). Recombination in evolutionary genomics. *Annual*

Review of Genetics, 36(Volume 36, 2002):75–97.

Pryor, Y. and Lindo, J. (2023). Deconstructing Eurocentrism in skin pigmentation research via the incorporation of diverse populations and theoretical perspectives. *Evolutionary Anthropology: Issues, News, and Reviews*, 32(4):195–205.

Quillen, E. E., Norton, H. L., Parra, E. J., Lona-Durazo, F., Ang, K. C., Illiescu, F. M., Pearson, L. N., Shriver, M. D., Lasisi, T., Gokcumen, O., Starr, I., Lin, Y.-L., Martin, A. R., and Jablonski, N. G. (2019). Shades of complexity: New perspectives on the evolution and genetic architecture of human skin. *American Journal of Physical Anthropology*, 168(S67):4–26.

Ramachandran, S., Deshpande, O., Roseman, C. C., Rosenberg, N. A., Feldman, M. W., and Cavalli-Sforza, L. L. (2005). Support from the relationship of genetic and geographic distance in human populations for a serial founder effect originating in Africa. *Proceedings of the National Academy of Sciences*, 102(44):15942–15947.

Richards, M. P., Schulting, R. J., and Hedges, R. E. M. (2003). Sharp shift in diet at onset of Neolithic. *Nature*, 425(6956):366–366.

Richerson, P. J. and Boyd, R. (2005). *Not by Genes Alone : How Culture Transformed Human Evolution*. University of Chicago Press, Chicago.

Richerson, P. J., Boyd, R., and Henrich, J. P. (2010). Gene-culture coevolution in the age of genomics. *Proceedings of the National Academy of Sciences*, 107(Supplement 2):8985–8992.

Rifkin, R. F., Dayet, L., Queffelec, A., Summers, B., Lategan, M., and d'Errico, F. (2015). Evaluating the photoprotective effects of ochre on human skin by in vivo SPF assessment: Implications for human evolution, adaptation and dispersal. *PLOS ONE*, 10(9):e0136090.

Robinson, M. R., Kleinman, A., Graff, M., Vinkhuyzen, A. A. E., Couper, D., Miller, M. B., Peyrot, W. J., Abdellaoui, A., Zietsch, B. P., Nolte, I. M., van Vliet-Ostaptchouk, J. V., Snieder, H., Medland, S. E., Martin, N. G., Magnusson, P. K. E., Iacono, W. G., McGue, M., North, K. E., Yang, J., and Visscher, P. M. (2017). Genetic evidence of assortative mating in humans. *Nature Human Behaviour*, 1(1):1–13.

Savage, P. E., Loui, P., Tarr, B., Schachner, A., Glowacki, L., Mithen, S., and Fitch, W. T. (2021). Music as a coevolved system for social bonding. *Behavioral and Brain Sciences*, 44.

Schrider, D. R. and Kern, A. D. (2017). Soft sweeps are the dominant mode of adaptation in the human genome. *Molecular Biology and Evolution*, 34(8):1863–1877.

Schuppli, C. and van Schaik, C. P. (2019). Animal cultures: How we've only seen the tip of the iceberg. *Evolutionary Human Sciences*, 1:e2.

Scrimshaw, N. S. and Murray, E. B. (1988). The acceptability of milk and milk products in populations with a high prevalence of lactose intolerance. *The American Journal of Clinical Nutrition*, 48(4 Suppl):1079–1159.

Ségurel, L. and Bon, C. (2017). On the evolution of lactase persistence in humans. *Annual Review of Genomics and Human Genetics*, 18(1):297–319.

Seielstad, M. T., Minch, E., and Cavalli-Sforza, L. L. (1998). Genetic evidence for a higher female migration rate in humans. *Nature Genetics*, 20(3):278–280.

Sharma, S. (2010). Assessing diet and lifestyle in the Canadian Arctic Inuit and Inuvialuit to inform a nutrition and physical activity intervention programme. *Journal of Human Nutrition and Dietetics*, 23(s1):5–17.

Shaw, B. (2016). The massim region of papua new guinea: A review and proposed chronology. *Journal of Pacific Archaeology*, 7(1):106–125.

Shaw, B. and Langley, M. C. (2017). Investigating the development of prehistoric cultural practices in the Massim region of eastern Papua New Guinea: Insights from the manufacture and use of shell objects in the Louisiade Archipelago. *Journal of Anthropological Archaeology*, 48:149–165.

Shennan, S. and Sear, R. (2020). Archaeology, demography and life history theory together can help us explain past and present population patterns. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376(1816):20190711.

Simon, A. and Coop, G. (2024). The contribution of gene flow, selection, and genetic drift to five thousand years of human allele frequency change. *Proceedings of the National Academy of Sciences*, 121(9):e2312377121.

Simoons, F. J. (1969). Primary adult lactose intolerance and the milking habit: A problem in biological and cultural interrelations. *The American Journal of Digestive Diseases*, 14(12):819–836.

Sokal, R. R. (1988). Genetic, geographic, and linguistic distances in Europe. *Proceedings of the National Academy of Sciences*, 85(5):1722–1726.

Sperber, D. (1996). *Explaining Culture: A Naturalistic Approach.* Blackwell, Oxford.

Strassberg, S. S. and Creanza, N. (2020). Cultural evolution and prehistoric demography. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376(1816):20190713.

Stubbersfield, J. M. (2022). Content biases in three phases of cultural transmission: A review. *Culture and Evolution*, 19(1):41–60.

Swallow, D. M. (2003). Genetics of lactase persistence and lactose intolerance. *Annual Review of Genetics*, 37(1):197–219.

Thompson, J. N. (1989). Concepts of coevolution. *Trends in Ecology & Evolution*, 4(6):179–183.

Tishkoff, S. A., Reed, F. A., Ranciaro, A., Voight, B. F., Babbitt, C. C., Silverman, J. S., Powell, K., Mortensen, H. M., Hirbo, J. B., Osman, M., Ibrahim, M., Omar, S. A., Lema, G., Nyambo, T. B., Ghori, J., Bumpstead, S., Pritchard, J. K., Wray, G. A., and Deloukas, P. (2007). Convergent adaptation of human lactase persistence in Africa and Europe. *Nature Genetics*, 39(1):31–40.

Uchiyama, R., Spicer, R., and Muthukrishna, M. (2021). Cultural evolution of genetic heritability.

Behavioral and Brain Sciences, pages 1–147.

Ulijaszek, S. (2018). Nutritional anthropology. In *The International Encyclopedia of Anthropology*, pages 1–10. John Wiley & Sons, Ltd.

van Oven, M., Brauer, S., Choi, Y., Ensing, J., Schiefenhövel, W., Stoneking, M., and Kayser, M. (2014). Human genetics of the Kula Ring: Y-chromosome and mitochondrial DNA variation in the Massim of Papua New Guinea. *European Journal of Human Genetics*, 22(12):1393–1403.

Voight, B. F., Kudaravalli, S., Wen, X., and Pritchard, J. K. (2006). A map of recent positive selection in the human genome. *PLoS biology*, 4(3):e72.

Waddington, C. H. (1942). Canalization of development and the inheritance of acquired characters. *Nature*, 150(3811):563–565.

Waddington, C. H. (1953). Genetic assimilation of an acquired character. *Evolution; international journal of organic evolution*, 7(2):118–126.

Waring, T. M. and Wood, Z. T. (2021). Long-term gene–culture coevolution and the human evolutionary transition. *Proceedings of the Royal Society B: Biological Sciences*, 288(1952):20210538.

White, L., Romagné, F., Müller, E., Erlebach, E., Weihmann, A., Parra, G., Andrés, A. M., and Castellano, S. (2015, 2015). Genetic adaptation to levels of dietary selenium in recent human history. *Molecular Biology and Evolution*, 32(6):1507–1518.

Whitehead, H. (2017). Gene–culture coevolution in whales and dolphins. *Proceedings of the National Academy of Sciences*, 114(30):7814–7821.

Whitehead, H., Laland, K. N., Rendell, L., Thorogood, R., and Whiten, A. (2019). The reach of gene–culture coevolution in animals. *Nature Communications*, 10(1):2405.

Whiten, A. (2021). The burgeoning reach of animal culture. *Science*, 372(6537):eabe6514.

Wilde, S., Timpson, A., Kirsanow, K., Kaiser, E., Kayser, M., Unterländer, M., Hollfelder, N., Potekhina, I. D., Schier, W., Thomas, M. G., and Burger, J. (2014). Direct evidence for positive selection of skin, hair, and eye pigmentation in Europeans during the last 5,000 y. *Proceedings of the National Academy of Sciences*, 111(13):4832–4837.

Wiley, A. S. and Cullin, J. M. (2016). What do anthropologists mean when they use the term biocultural? *American Anthropologist*, 118(3):554–569.

Williamson, S. H., Hubisz, M. J., Clark, A. G., Payseur, B. A., Bustamante, C. D., and Nielsen, R. (2007). Localizing recent adaptive evolution in the human genome. *PLOS Genetics*, 3(6):e90.

Yamaguchi, Y. and Hearing, V. J. (2009). Physiological factors that regulate skin pigmentation. *BioFactors (Oxford, England)*, 35(2):193–199.

Yengo, L., Robinson, M. R., Keller, M. C., Kemper, K. E., Yang, Y., Trzaskowski, M., Gratten, J., Turley, P., Cesarini, D., Benjamin, D. J., Wray, N. R., Goddard, M. E., Yang, J., and Visscher, P. M. (2018). Imprint of assortative mating on the human genome. *Nature Human Behaviour*, 2(12):948–954.

Yılmaz, F., Karageorgiou, C., Kim, K., Pajic, P., Scheer, K., Human Genome Structural Variation Consortium, Beck, C. R., Torregrossa, A.-M., Lee, C., Gokcumen, O., Audano, P. A., Austine-Orimoloye, O., Beck, C. R., Eichler, E. E., Hallast, P., Harvey, W. T., Hastie, A. R., Hoekzema, K., Hunt, S., Korbel, J. O., Kordosky, J., Lee, C., Lewis, A. P., Marschall, T., Munson, K. M., Pang, A., and Yilmaz, F. (2024). Reconstruction of the human amylase locus reveals ancient duplications seeding modern-day variation. *Science*, 0(0):eadn0609.

Zeder, M. A. (2018). Why evolutionary biology needs anthropology: Evaluating core assumptions of the extended evolutionary synthesis. *Evolutionary Anthropology: Issues, News, and Reviews*, 27(6):267–284.

Zeng, T. C., Aw, A. J., and Feldman, M. W. (2018). Cultural hitchhiking and competition between patrilineal kin groups explain the post-Neolithic Y-chromosome bottleneck. *Nature Communications*, 9(1):2077.

Zhang, C., Li, J., Tian, L., Lu, D., Yuan, K., Yuan, Y., and Xu, S. (2015). Differential natural selection of human zinc transporter genes between african and non-african populations. *Scientific Reports*, 5(1):9658.