Cultural Evolution and Population Health Interventions

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Abstract

Culture is often invoked as an explanation for disparities in health or as a barrier to success in population health interventions, yet the micro-level processes underpinning cultural inertia and cultural epidemics are rarely unpacked. By contrast, a cultural evolution framework breaks down "culture" as a population of cultural variants and focuses on uncovering the social learning "strategies" and individual motivations leading to behavioural variation and change. Here I elaborate on how thinking evolutionarily can help understand the bidirectional relationship between behaviour and culture, thereby shedding light on the processes leading to the adoption, transmission, and maintenance of behaviour over time and across socio-ecological contexts. I begin with introducing the concept of culture in epidemiology as well as contemporary evolutionary approaches to culture. I then consider how a cultural evolution framework can be deployed at various levels of interventions, from health-message framing and norms-based messaging to social network and communities-based interventions. Lastly, I evaluate how a cultural evolution framework can be harnessed to tackle public health challenges, including how to seed a new healthy behaviour, how to spread behaviour beyond its initial uptake and how to maintain behaviour in the face of changing ecologies. While cultural evolution (CE) studies of population health (PH) issues are currently limited, there is a large scope for CE and PH to mutually benefit from joining forces.

Introduction

Culture as a challenge for population health

Despite the huge success of past public health efforts against infectious diseases through health infrastructure, scientific discovery and social reforms, contemporary population health interventions are struggling to tackle "lifestyle" diseases (e.g., depression, cancer, obesity) and promote health behaviour change (e.g., vaccination, sanitation, medication adherence, contraceptive uptake). Notwithstanding the importance of social circumstances in producing ill health in the first place, a central challenge to contemporary population health in both developing and developed contexts is understanding why people behave the way they do (Kelly & Barker, 2016).

Behaviour is partly shaped by *culture*, which can be broadly defined as a set of shared ideas, values, customs, and technologies. The concept of culture in epidemiology dates back from 1950s-60s (Hruschka, 2009) and has increased in frequency ever since (Fig. 1), as in other fields, but is often conceptualised as a barrier to public and global health (e.g. in 44% of papers invoking culture as an explanation in epidemiology, Hruschka, 2009). Public health issues often seem intractable "*due to their roots in deeply grounded cultural practices that appear unassailable.*" (Raymond et al., 2014). According to Hrushka (Hruschka, 2009), 'culture' is invoked in epidemiology articles as a residual explanation, "proposed [only] 'to do something' that could account for disparities in health, while the precise pathways are seldom specified".

By contrast, an evolutionary approach to culture approaches culture dynamics the way epidemiologists approach the diffusion of infectious diseases, asking about the "susceptibility" to and "infectivity" of a cultural trait, its route(s) of transmission (individual-to-individual, one-to-many) and "recovery" rates (Cavalli-Sforza, L.L. & Feldman, 1981; Sperber, 1996) although through different processes (Centola, 2010). This dynamic framework seems well fitted to contribute a novel perspective on public health interventions because it studies the mechanics of cultural transmission, focusing on the cognitive, social, and ecological factors leading to both "culture inertia" and "cultural epidemic", two opposite views on culture change.

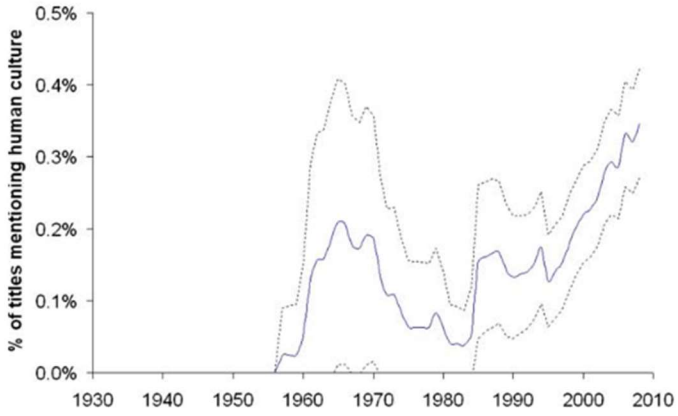

Figure 1. Use of "culture" or "cultural" in titles in top epidemiology and population health journals (10-year moving average, with 95% confidence intervals). Taken from (Hruschka, 2009)

The modern cultural evolution framework

Modern cultural evolution is divorced from 19th centuries western-centric views of cultural evolution (Haas, 1998) according to which "cultures" or populations, in the sense of cultural anthropology, were ranked on a ladder of varying levels from barbarism to civilization, characterized by intrinsic directionality and progress. By contrast, within the framework of modern cultural evolution, which kept the idea that culture is learned, culture is defined in atomic rather than essential terms, considering how the frequency of **cultural variants** (e.g., the preference for low fertility, the use of vaccines and contraceptives) changes over time in populations.

The metaphor of "cultural variants" has been disputed (Fracchia & Lewontin, 1999), however, "*because every historical phenomenon has its own particular locus in a particular sociocultural constellation with its own concrete and particular time and history*". Further, how faithfully a cultural variant is transmitted through imitation has been debated (Godfrey-Smith, 2012). Notwithstanding the complexity of how cultures come about, in the context of public health concerns (vaccination, contraception, health behaviour), it is helpful to use the metaphor of **cultural variants** to better understand whether and how

they are **transmitted** between individuals and the extent to which culture change is the result of **biased social transmission (i.e., cultural selection).**

Cultural evolution vs. an evolutionary approach to culture

In the *narrow sense*, "cultural evolution" is the study of the Darwinian process leading to change in the distribution of **culturally transmitted** variants over time through social learning (Boyd & Richerson, 1985; Cavalli-Sforza, L.L. & Feldman, 1981), independently of their effects on individual biological fitness in current environments. This process has been invoked for explaining the spread of potentially maladaptive outcomes, such as contraception and the demographic transition (P. J. Richerson & Boyd, 2004). Models posit that the ability to learn from each other, which dramatically lowers the cost of acquiring ecologically-relevant information, specifically in unstable or stochastic environments, allows rapid adaptation to a wide range of environments (Boyd et al., 2011). Empirical evidence suggests that humans are particularly good at using social information and imitating (Henrich & McElreath, 2012), and cultural pressures have led to the evolution of social **learning strategies** (e.g. prestige-biased transmission, conformist biased transmission, kin-biased transmission) enabling humans to make adaptive decisions about when to copy and who to copy (Boyd & Richerson, 1985; Henrich & McElreath, 2012). According to the costly information hypothesis (Henrich & McElreath, 2012), **social learning** is particularly adaptive when the cost to acquire information individually is high, which is often invoked in the case of health behaviour (Acerbi, 2020). Further, while transmission biases might be adaptive in small-scale societies, novel environments might lead to maladaptive dynamics such as the spread of misinformation and harmful beliefs if prestigious individuals do not possess relevant information (Moya et al., 2020) and/or if the availability of information about popularity is distorted (de Barra, 2017).

In the *broad sense*, cultural evolution encompasses the study of cultural change over various timescales, independently of cultural transmission mechanisms. In this view, culture does not necessarily evolve in the Darwinian sense, but can nevertheless change due to the selection of some traits over others, which can then influence cultural transmission processes. For instance, some health practices might achieve widespread acceptance, i.e., enjoy "cultural success", primarily because they are intuitively appealing

to individuals, often despite being maladaptive. On the one hand, evolutionary psychologists have invoked the importance of innate cognition (universal cognitive features acquired through human evolution such as "folk psychology" and "folk biology") for explaining the spread of pseudoscience (Boudry et al., 2015), cross-cultural practice of bloodletting (Miton et al., 2015) and vaccine beliefs (Salali & Uysal, 2020). On the other hand, behavioural ecologists start from the premise that evolved cognitive processes optimize individual fitness given ecological parameters, favouring the transmission of behaviour that is adaptive in a given cultural ecology. The focus is on inter-individual variation in the fitness costs and benefits of adopting or continuing a given practice across the diffusion curve. This approach has been used to study cultural change within generations, to understand who the first adopters of contraceptive methods are (Alvergne & Stevens, 2021), or why female genital cutting (FGC) might persist (Howard & Gibson, 2017).

To contribute to public health issues, an evolutionary perspective to culture in population health requires **a broad-church approach** to account for both why and how the frequency of given cultural traits change over time. In this way, the process of cultural change is considered within a **multi-level framework**, integrating cultural transmission processes and evolutionary constraints on behaviour (evolved behavioural dispositions to maximize reproductive success given socio-ecological contexts, evolved cognitive learning mechanisms, innate folk psychology). Next, I draw parallels between cultural evolution studies and the population health literature at multiple levels of interventions, from individual to social networks and communities. I then apply a cultural evolution framework to the various stages of the diffusion process, including the emergence, spread, stall, oscillations, and disappearance of cultural variants. I focus not only on public health behaviours such as contraceptives or vaccines but also on sustainable behaviour, as the challenges of global health are inextricably linked to the climate change crisis (Cousins et al., 2021).

Population health interventions from a cultural evolution perspective

Population health has long recognized that interventions should be rolled out at several levels to tackle social inequalities, **strengthening the individual, relational and group levels** (Whitehead, 2007). A cultural evolution framework will integrate those levels together including cognitive universals shaping individuals folk knowledge and reasoning (Atran, 1998), social learning strategies shaping cultural transmission networks (Mesoudi, 2016), and differential success across communities (cultural group selection processes (P. Richerson et al., 2016)). In this way, a cultural evolution approach can help understand both motivations for public health behaviour and the mechanisms underpinning cultural variation within and between populations. Such system approach (Buskell et al., 2019) is useful for determining how to tailor levels of interventions to the ideal and technology to promote.

Individual-based interventions: understanding motivations

Health messages framing

Campaigns aimed at the individual level have traditionally followed a "deficit model", where the cause of individual "unhealthy" behaviour is rooted in a lack of knowledge, competence, skill, or power. To address this, individual based interventions have used campaigns aimed at improving the health education of individuals, through mass media campaigns, skill building group as well as one-to one counselling (Whitehead, 2007). Critical to this approach is the **Health Belief Model**, the most used theoretical framework focusing on individual perception of risks, benefits, barriers, susceptibility to disease and self-efficacy (Abraham & Sheeran, 2015). However, the health belief model, although useful, has limited power for predicting and changing a range of healthy behaviours (Abraham & Sheeran, 2015): improving one's health is often a weak motivator. For instance, studies aiming at increasing handwashing, a key practice to tackle diarrhea and reduce child mortality, found that one of the strongest predictors of handwashing with soap was related to nurturance, social acceptance, and disgust of latrines, but not health (Scott et al., 2007). Here "scientific" and "evidence-based" information about the health payoffs of

adopting a public health practice (e.g., vaccine, smoking cessation) might not appeal to intrinsic motivations and limit cultural transmission. For instance, while vaccine acceptance is predicted by COVID-19-related anxiety as well as perceived risk of catching COVID-19, "*Scientific information, such as vaccines are safe, are often not intuitive, making them harder to be disseminated*" (Salali & Uysal, 2020).

Deciding how to frame an information requires understanding what makes the content of a cultural trait "attractive" because it has implications for **content-biased cultural transmission**. First, motivations to increase one's sexual attractiveness, status, social support, and other outcomes directly linked to fitness have likely been favoured over our evolutionary history (Saad & Peng, 2006), and might conflict with "healthy" behaviour. For instance, a study (n=147 young female adults) examined the use of appearance-based message for reducing the use of sun tanning, a behaviour responsible for a sharp rise in skin cancers in the US. As compared to a control group receiving standard information based on the link between UV radiation and melanoma, the group exposed to appearance-based messages on the impact of the UV on skin ageing were 50% less likely to use UV up to 2 months following the experiment (JJ Hillhouse & Turrisi, 2002) and similar framing effect were replicated among adolescents (Joel Hillhouse et al., 2017). In 2012, the skin UK Cancer charity has rolled out this idea through the R UV Ugly campaign, which performed 1648 UV skin scans in shopping centers across the country to show users of sun tanning the cosmetic damage of UV over- exposure (https://www.iccp-portal.org/r-uv-ugly). The evaluation report indicates that 46% of respondents reported stopping using sunbeds or using sunbeds less than eight weeks after the campaign (*R UV UGLY Evaluation Report*, 2012). What remains to be investigated is whether the cultural transmission of decisions about sun tanning is promoted by the intervention highlighting the cost of tanning for attractiveness. More generally, health messages campaigns might benefit from investigating framing that can promote **content-based social transmission** (Mesoudi & Whiten, 2008) considering the importance of our evolved cognition to be attracted to content relevant to fitness payoff across our evolutionary history.

Norm-based interventions

A key public health approach has been to use norm-based messaging to change "norms", which can be defined as the behavioural standards shared and enforced by a community, although the definition of norms is highly variable across disciplines (Legros & Cislaghi, 2020). Norms have been linked to a wide variety of health-related behaviours, from contraception to vaccines (Valente, 2010) and climate-change related behaviour (Cialdini & Jacobson, 2021), as well as harmful ones (e.g. female genital cutting (Howard & Gibson, 2017; Vaitla et al., 2017)). The first public health efforts to change norms were mainly based on the theory of **Planned Behaviour's subjective norm** concept (Ajzen, 1991), the perceived social pressure to perform a behaviour, and consists in social marketing strategies displaying information about other's behaviour (Tankard & Paluck, 2016) and group discussions (Cislaghi, 2018; Vaitla et al., 2017). Subsequently, population health efforts have been informed by **the Focus Theory of Normative Conduct** (Kallgren et al., 2000), which distinguishes between norms that are descriptive (perception of a behaviour's prevalence) and those that are injunctive (perception of group's approval). One can draw a parallel with the cultural evolution literature, which distinguishes between **unbiased frequency-dependent transmission** (random copying) **and biased frequency-dependent transmission** (conformity), i.e., the disproportionate tendency to copy the majority.

The study of **conformity** is of great interest to CE because of the benefits of norms for reinforcing coordination between group members (McElreath et al., 2003). Gene-culture theory posits that interactions between our cultural and genetic inheritance systems may have favoured prosociality, including the cognitive foundations for large-scale cooperation such as internalized desires to follow and enforce norms: so called culture-gene coevolved norm-psychology (Chudek & Henrich, 2011). The evolution of normative motivations 'to do the right thing' (i.e. intrinsic motivations, including non-moral rules of etiquette (Davis, Hennes, and Raymond 2018)), a different concept from just following norm because of sanction or social reward (instrumental motivation), is argued to be a unique outcome of gene-culture coevolution. Social learning through intrinsic normative motivations (maintained by internal sanction such as shame or guilt rather than external material sanctions) appear to be more effective than instrumental learning for acquiring adaptive

knowledge (Gintis, 2003). Understanding whether people engage with sustainable behaviour because "it's the right thing to do" (intrinsic normative motivations) or because they gain some benefit from adhering to this norm has implications for thinking through how incentives can be used together with norms, as instrumental motivations (cash payments) can crowd out normative motivations (civic duty) – in some contexts, making healthy behaviour more noticeable will be more influential than cash transfer (Davis et al., 2018).

A key finding from CE is that information about the frequency of a behaviour, such as the level of approval for a given practice, can be inaccurate because not all decisions are observed or reported equally, contributing to the spread false beliefs and/or the maintenance of ineffective treatments. In a study of online reviews for a brand of food products marketed to lower cholesterol, online reviews rated the effects of the product on health 3 times more positively than expected based on the scientific literature, because people with positive experiences were more likely to leave a review (de Barra, 2017). This **reputational distortion** of the information was also found for weight loss and fertility treatments (de Barra et al., 2014). This bias in the availability of information (of the observability of behaviour) is critical in population health interventions, namely: are unhealthy behaviours (going in the park while supposed to isolate at home) more visible than public health ones (staying at home)? When unhealthy attitudes are overestimated while health attitudes are underestimated, it might be helpful to draw attention to the commonality of healthy practices.

Network-based interventions: understanding cultural transmission

Network-based interventions focus on harnessing social relations for information passing. For instance, theorists suggest that to change a social norm it is critical to reach out to people's **"reference group**," (Cislaghi et al., 2019). In a study on towel reuse by hotel clients, participants were more likely to comply if they were told that prior occupants of the room did comply (Goldstein et al., 2008). In this line, recent innovative female empowerment campaigns have banked on idea of "**organized diffusion**", where participants shared their knowledge to chosen other members of the community, usually

a family member or a friend (Vaitla et al., 2017). While the **theory of planned behaviour** collects data on reference groups by asking about "people who are important to you" (Shakya et al., 2014) or use boundaries such as villages, a cultural evolution perspective suggests focusing on multiple social relations, as various learning strategies could be harnessed, depending on context. Empirical and modelling work show that people do not learn randomly but preferentially learn from relatives (kin-based), knowledgeable (prestigious such as experts and celebrities), as well as similar (based on age, gender or accent) individuals (Efferson et al., 2016). For instance, people choose people who are similar to them in online health social networks (Centola & van de Rijt, 2015). Those are known as "**context-dependent model bias**" (Mesoudi, 2016), where the source, rather than the content of information or its frequency in the population, is key for understanding the transmission of cultural variation. Not considering the importance of transmission sources can lead to the failed adoption of health behaviour (Moya et al., 2020).

One relevant context-dependent model bias for population health interventions is **prestige-biased transmission**, as exemplified by the recent UK government strategy to enlist influencers on social media as well as "sensible celebrities" to spread pro-vax messages (Du-Lieu & Grassi, 2020). There are many examples suggesting that that celebrity endorsement campaigns are successful (e.g. Elvis Presly and the polio vaccine, the Angelina Jolie effect on genetic testing for the BRCA1 mutation), however their effects might result from accessibility of information interacting with prior motivations (Acerbi, 2020). Further, in conditions of rapid change, prestige-biased transmission might lead to the spread of misinformation if prestigious people are not expert of the problem at hand (Moya et al., 2020). Prominent public figures play an outsized role in spreading misinformation about COVID-19: the online content produced by prominent people is disproportionately engaged with or shared on social media (Brennen, Simon, Howard, & Nielsen, 2020, Figure 2). While prestige does not affect the transmission of novel controversial arguments in experiments where individuals possess little preexist opinion (Jiménez & Mesoudi, 2020), the situation might differ when most individuals have prior experience with health behaviour and the technologies to achieve it. Interaction between prestige model-based bias with negative content bias can make the negative message about vaccines (or any other technology)

transmitted by celebrities (Djokovic) and experts (e.g., Pr Raoult) particularly likely to spread (Jiménez & Mesoudi, 2020).

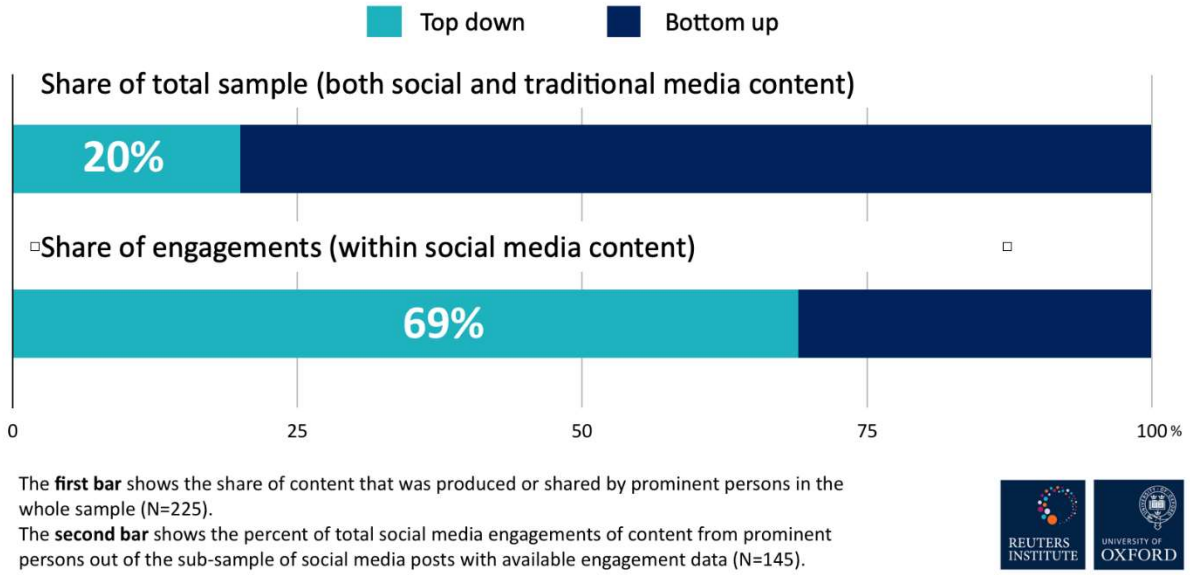

Figure 2. Top down versus bottom-up information. Adapted from (Brennen et al., 2020)

Note that the success of network interventions might be constrained by the ecology, because there are complex feedbacks between **network structure** and cultural evolution (Smolla & Akçay, 2019). In highly connected populations, information can spread faster and further than in populations connected through long ties only (complex contagion processes (Centola, 2010)). This is the case for toilets adoption where variation in the rates of adoption of latrines across communities depends on the degree of social clustering (Shakya et al., 2015). Further, different ecological pressures might require different types of cultural adaptations and thus different network structures are expected to evolve across ecologies (Smolla & Akçay, 2019). Interestingly, social learning vary cross-culturally across subsistence modes, where pastoralists rely more on social information than on individual information as compared to horticulturalists (Glowacki & Molleman, 2017; Mesoudi et al., 2016). This suggests adapting network interventions to the local network structure.

Community-based interventions: understanding cultural group selection

First, kin-biased transmission might be harnessed in community-based interventions (CBI) focusing on community as the "resource", where the importance of community ownership of a given intervention is emphasized (McLeroy et al., 2003). For instance, a campaign aiming at increasing the treatment coverage against onchocerciasis in populations of Uganda compared the effectiveness of classic community-directed treatment with ivermectin (CDTI) and kinship enhanced CDTI, where the community distributors were sensitised to provide services only within their respective kinship zones. They found that household respondents from kinship enhanced CDTI reported better performance than classic CDTI on treatment coverage and the mobilization for CDTI activities (Katabarwa et al., 2010). Here kinship represents a network of individuals connected by blood and marriage, and serves as a "platform", where interactions "promote the adoption of healthy behaviour which can passed on to future generations" (Katabarwa et al., 2010).

Second, using a Cultural Multilevel Selection (CMLS) framework might inform CBI focusing on community as the "agent" of change. Cultural Multilevel Selection (CMLS) considers together competition between individuals within groups, among groups of individuals and among groups of groups (Wilson & Sober, 1994). In this framework, group beneficial behaviours norms and institutions are favoured when cultural group selection pressures are stronger than individual level selection pressures. Through the differential imitation of more successful groups, practices that are costly at the individual level can spread. In a study on the adoption of sustainable management practices in California viticulture, Hillis et al. (2018) found a disproportionate imitation of successful groups as some growers imitate the practice of growers from more successful regions. Therefore, information about the success of other groups might help spread novel behaviours through CMLS. Beyond sustainable agricultural practices, one could apply the same logic to public health concerns by manipulating group benefit (e.g., by using public health certification programs for groups of doctors or practitioners, as well as informing about what other groups are doing). More generally, model communities may create important opportunities for imitation by others, in a manner consistent with cultural selection mechanisms (Davis et al., 2018).

Through the diffusion curve: tackling population health issues with cultural evolution

Population health interventions aiming at "changing culture" must overcome various obstacles to successfully deliver their objective of bettering population health. After conducting qualitative work essential to contextualize the social, economic and political ramifications associated with a given "healthy" behaviour to be promoted, population health interventions designers must tackle various problems, such as (i) how to seed a new behaviour given the local socio-cultural context, (ii) how to spread a behaviour beyond its initial uptake and beyond the majority or some tipping point, (iii) how to maintain a behaviour in the face of changing ecologies (e.g. when the epidemiological situation changes; when rumours spread). Given this, breaking down "culture" as a population of cultural variants is helpful for linking micro-level processes to macro-level change.

Seeding a novel trait in a population: who are the first adopters?

Understanding who the first adopters are, both their motivations and their structural properties (i.e., position in social networks), is key for predicting whether, how and how fast a cultural variant might spread successfully.

Innovations that spread successfully are often first adopted by opinion leaders, those who are at the centre of interpersonal communication networks (hubs) and hold more trustworthy information (Rogers, Everett, 2003). It is often unclear whether their action is through information passing or through decision passing, however. In a study on the uptake of microfinance loans in 43 villages in South India (Banerjee et al., 2013), first informing individuals with high centrality (connected to people who are also well connected), thus at the centre of communication networks, positively influences the spread of participation in the microfinance scheme. Among the leaders chosen as injection points, those who were also centrally positioned across multiple networks were both more likely to participate in the scheme and 4 times more likely to transmit the information to their neighbours, suggesting prestige-biased transmission of information. However, the role of opinion leaders in passing decisions, rather than just information, is unclear. In a 2019 Cochrane review involving 337 hospitals, 350 primary care practices, 3005 healthcare

professionals, and 29,167 patients, there is only moderate empirical support for the role of local opinion leaders in improving the ability of professionals to follow evidence-based guidelines, with an uncertain impact on patient outcomes (Flodgren et al., 2019).

When early adopters differ from opinion leaders, innovations are expected to spread more slowly. In a study on contraceptive uptake my colleagues and I conducted in rural areas of Ethiopia we found that in the early stages of the diffusion process (prevalence < 20%), the first adopters were those women who had the highest reproductive output (highest fertility and shorter inter-birth intervals) for their age, while none of their close acquaintances were users themselves (Alvergne et al., 2011). By adopting contraception, those women avoided short 1-year inter-birth intervals (Alvergne et al., 2013), which historically is associated with increased child mortality. This situation might not be generalizable to other populations, but it shows that the initial rise in frequency, even up to 20%, can sometimes be explained by individual level cognitive mechanisms evolved to adjust reproductive scheduling in a way that maximizes reproductive success given the socioecology, without invoking social transmission. The fact that early adopters were not opinion leaders also partly explain why the diffusion of contraceptive use somewhat stalled, as prestige-biased transmission could not operate.

Another way to choose injection points is to target cohesive groups, rather than individuals, to bank on frequency-dependent transmission of decisions through endorsement. The influence of endorsement might be particularly relevant for health-related behaviours, who need social reinforcement to spread because individual learning is potentially costly (Centola, 2020). In this case, it might be pertinent to pass on information to individuals belonging to clusters of individuals with high network cohesion (high density of connection). In a study of latrine ownership in 75 Indian villages, cohesive networks predicted no ownership of latrines, suggesting an important role of endorsement for the decision to own latrine (Shakya et al., 2015). Combined with the empirical and simulation findings that behaviour, compared to infection, spreads through wide bridges (reinforcement through multiple sources of exposure (Centola, 2020)) rather than long ties (distant connections), introducing information to groups of highly interconnected individuals might be an effective strategy if it increases the share of close contacts deciding to change behaviour based on the information.

Spreading new norms that are costly at the individual level

Many public health norms represent **cooperative dilemmas**, where a measure is beneficial for the group but not necessarily for the individual, such as in the case of vaccination or sustainable behaviour. In this context, gene-culture theory suggests harnessing our norm psychology, a set of cognitive traits evolved through cultural selection on cooperative behaviour (Davis et al., 2018). This leads to the evolution of intrinsic normative motivations, which include the motivation to both "do the right thing" and enforce a normative behaviour on others. In turn, such motivations lead to the imitation of the most frequent and trending behavioural trait (Davis et al., 2018). Such approach is already implicit in norms-based messaging (see previous section) but could be extended through increased awareness of new policies, actions (e.g., court ruling gives the perception of public support which can then cascade), and behaviour (drawing attention to individuals who perform the behaviour). Normative motivations can also be mobilised in norm reframing, where support for a behaviour is reframed as support for another important existing norm (Davis et al., 2018) (e.g., what if we reframe vaccination as a behaviour consistent with norms of masculinity?). Finally, it is important to evaluate the degree of shared identity between community members and the greater society (Smaldino et al., 2017), as it will limit the potential for social learning. Note that one must understand heterogeneity in individual costs, as it will influence the scope for cooperative motivations to influence behaviour. For instance, one can frame vaccination as prosocial rather than individual at the beginning of a pandemic (Jordan et al., 2021), but it might be phrased in relation to individual benefit as vaccination coverage increases, as it becomes non rational for individuals to vaccinate (C. T. Bauch & Earn, 2004).

Tackling the maintenance of harmful behaviour

Is culture as defined by frequency-dependency-behaviour an explanation for the persistence of practices? Some frequency-dependent bias, such as conformity bias, are often invoked to explain the spread of neutral behaviour or the maintenance of costly behaviours (P. J. Richerson & Boyd, 2004). While a cultural evolutionary framework is agnostic about the impact of behaviour on fitness, some practices including female genetic cutting (FGC) or intimate partner violence are puzzling, as they potentially bring about fitness costs, and thus a complete evolutionary account

should consider how cultural evolutionary processes interact with evolved dispositions to maximize lifetime reproductive success. Such an integrative approach has been used to investigate the persistence of FGC, the partial or total removal of female genitalia and an enduring puzzle for policymakers taking place in 29 countries in Africa and the Middle East. Using demographic and health surveys from 5 African countries, Howard and Gibson (2017) consider the extent to which FGC relates to reproductive success as a function of the cultural context. They show that FGC is an adaptive frequency-dependent practice. First, the probability of daughters cut covaries with the frequency of FGC in that group. Second, in social groups where the practice is in high frequency, women with FGC and aged 40-49 years have a higher number of surviving offspring than their uncut peers on average, but the reverse is true in groups where FGC is in lower frequency (<30%) (Fig. 3A). Finally, the predicted probability of a mother having a cut daughter increases linearly with the frequency of FGC in the mother's ethnic group. Because the diffusion curve is not S-shaped (Fig. 3B), a pattern expected in the presence of conformity effects, but rather displays a constant rate of change through time, the findings imply that "*FGC eradication initiatives based on the idea of a tipping point driving behavioural change may not be the only solution. Instead, a piecemeal reduction of FGC by individuals can play a part in the decline of FGC prevalence in the overall population.*"

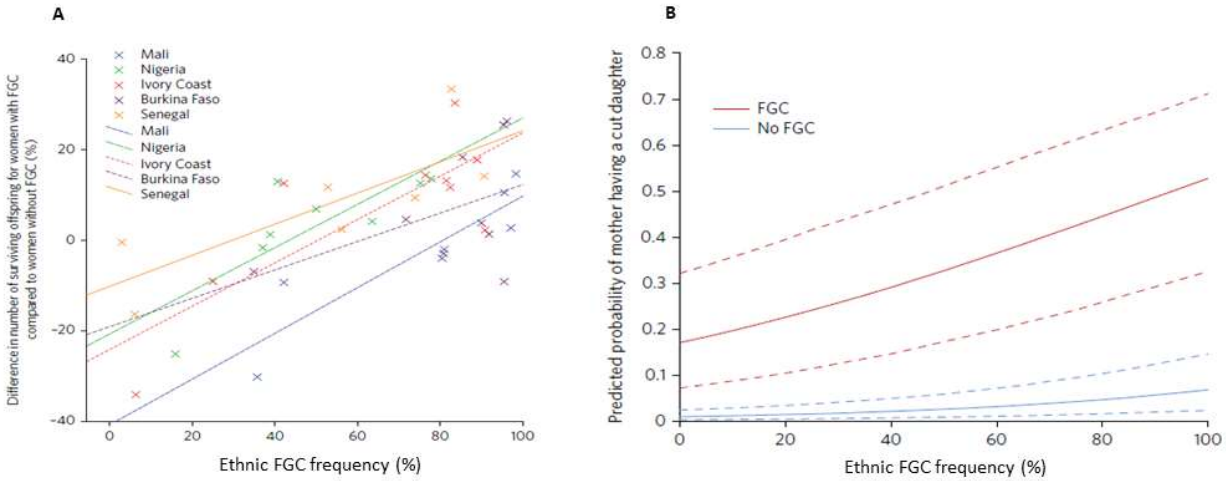

Figure 3. A) Correlation between ethnic FGC frequency and the percentage difference in average number of surviving offspring for women aged 40-49 years with FGC compared to women without FGC. Mali: n = 1650; Ivory Coast: n = 847; Burkina Faso: n = 2512; Nigeria: n = 2274; Senegal: n =1866. **B)** Predicted probabilities of having a cut daughter by mother's FGC status at different ethnic FGC frequencies. Adapted from (Howard & Gibson, 2017).

Coevolutionary dynamics

As cultural change unfolds, so does the socio-ecology of the cultural variant, which can in turn cause a decrease or oscillations in the prevalence of behaviour. For instance, adopting a health technology (contraception, vaccination) might lead to side-effects, leading to discontinuation behaviour and the spread of information about side-effects (Alvergne & Stevens, 2021). Further, the population increase of a given behaviour can change individual payoffs (when the benefit of vaccination decreases with herd immunity) and opportunities for social transmission. To tackle such cultural evolution dynamics, it is useful to recognize several patterns of transmission co-evolving, such as the transmission of infectious disease with the transmission of vaccination behaviour, or the transmission of contraceptive uptake with the transmission of contraceptive discontinuation.

There is a dynamic relationship between the spread of infection and infection-preventing behaviour, leading to oscillations. Upon disease outbreak, wearing face masks, isolating, or vaccinating can protect individuals and communities. As disease becomes less prevalent, such as when vaccination coverage increases, the incentive to vaccinate decreases as unvaccinated individuals are less likely to be infected due to herd immunity (C. T. Bauch & Earn, 2004). The resulting oscillations in vaccination coverage (Fig. 4) have been mainly attributed to imitation dynamics (Bauch, 2005), where individuals copy the most successful strategies based on the infectious status of their neighbours. The discrepancy between the optimal behaviour for individuals and the optimal level of vaccination coverage to protect populations can lead to oscillations in vaccination coverage, jeopardizing efforts to eradicate infectious diseases under voluntary vaccination policies (C. T. Bauch et al., 2003; C. T. Bauch & Earn, 2004)(Bauch, 2003, 2004).

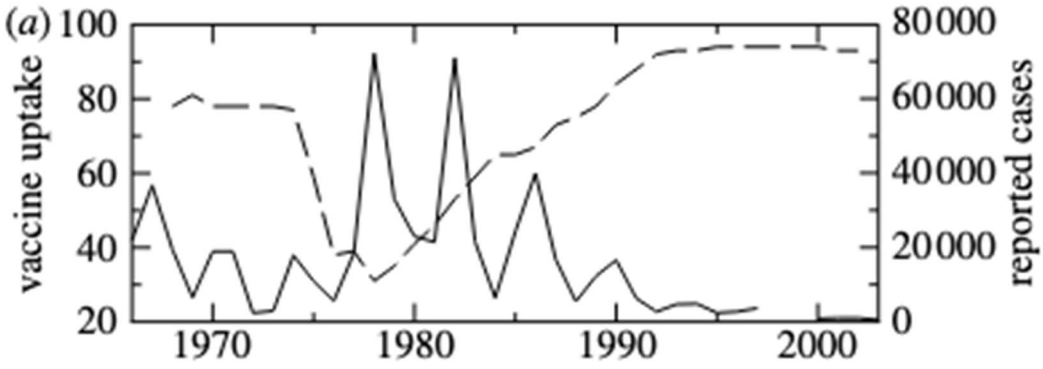

Figure 4. Pertussis vaccine uptake (dashed) and case notifications (solid) in England and Wales from 1967-2003. Adapted from (C. T. Bauch & Earn, 2004).

The importance of free-riding based on the perception of accurate risk and benefits is likely insufficient for explaining the dynamics of vaccination coverage (Voinson et al., 2015), because human decision-making is constrained by learning "strategies" or "bias" as well as opportunities for cultural transmission (the structure of social networks). In a behaviour incidence model, Voinson et al. showed that failure to eradicate vaccine preventable disease can be explained by cognitive biases that maintain heterogeneity in how people perceive risks and form an opinion (e.g., confirmation bias), rather than payoff or conformity-biases alone (Voinson et al., 2015). Further, the field of digital epidemiology has shown that vaccine sentiments spread within clusters, leading to pocket of unvaccinated individuals (Salathé & Bonhoeffer, 2008). Overall, one must consider whether behavior changes as a response to (i) disease epidemiology and perceived changes (e.g. with infection risks (prevalence elastic behavior)) and (ii) given opinions formed largely independently of disease prevalence (health-belief), such as in the case of pediatric vaccines decisions made in the absence of disease outbreak (Funk et al., 2009, 2010). Those dynamics can be faster than infectious disease dynamics.

The distinction between a behaviour (i.e., contraceptive behaviour) and the technology to achieve it is likely to matter for understanding how culture change. A case in point is contraceptive behaviour, where the same ideal (limiting family size) can be achieved through different technologies (e.g. condom, sterilization) or where the same technology

(e.g. the injectable contraceptive) enables different ideals (limiting total family size vs increasing interbirth interval to recuperate between births rather than limit total family size per se (Bledsoe et al., 1998)). In this context, a cultural evolution approach requires considering diversity in the transmission of both ideas and technologies (Alvergne & Stevens, 2021). When the use of technology leads to a negative bodily and/or social experience, discontinuation might ensue. In turn, information about negative experiences, for instance the type and severity of side-effects, can be transmitted and influence "naive" individuals not to adopt the behaviour and change the prevalence of the behaviour in the population. In this context, it is the diversity of technology that might best explained culture change rather than the diversity in ideals.

Conclusion

Contemporary population health rolls out interventions aimed at promoting some behaviours and practices, including healthy eating, contraception, and vaccination, while "eradicating" others, such as smoking, female genital cutting or open defecation. Yet, the success of such interventions is variable and sometimes compromised, depending on context, and "culture" is often invoked as an explanation for failing to meet population health objectives. Applying a cultural evolution framework can be useful to overcome cultural barriers because it requires breaking down culture into cultural variants, tracking their frequency over time and testing hypotheses about the role of individual motivations, social transmission networks and cultural group selection in shaping diffusion curves. Further, cultural evolution can be harnessed to distinguish questions about the "origin" (that is, the initial uptake or emergence of a novel cultural variant), and the "distribution" (that is, the rate of spread and maintenance of various cultural variants). While understanding motivations is key to answering both "origins" and "distributions" questions, imitation and other forms of cultural transmission are fundamental for understanding the distribution of cultural traits. The time is ripe for further cross talk between cultural evolution and population health.

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