Migration, acculturation, and the maintenance of between-group cultural variation

Alex Mesoudi *

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Abstract

How do migration and acculturation affect within- and between-group cultural variation? Classic models from population genetics show that migration rapidly breaks down between-group genetic structure. However, in the case of cultural evolution, migrants (or their children) can acculturate to local cultural behaviors via social learning processes such as conformity, potentially preventing migration from eliminating between-group cultural variation. To explore this verbal claim formally, here I present models that quantify the effect of migration and acculturation on between-group cultural variation, first for a neutral trait and then for an individually-costly cooperative trait. I also review the empirical literature on the strength of migrant acculturation. The models show that surprisingly little conformist acculturation is required to maintain plausible amounts of between-group cultural diversity. Acculturation is countered by assortation, the tendency for individuals to preferentially interact with culturally-similar others. Cooperative traits may also be maintained by payoff-biased social learning but only in the presence of strong sanctioning institutions. While these models provide insight into the potential dynamics of acculturation and migration in cultural evolution, they also highlight the need for more empirical research into the individual-level learning biases that underlie migrant acculturation.

Keywords: acculturation; cooperation; cultural evolution; cultural F_{ST}; migration

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

Introduction

Humans are behaviorally diverse, and much of this variation occurs between groups, societies or nations (1). Anthropologists and linguists have documented extensive behavioral and linguistic variation across human societies: approximately 6800 languages are spoken worldwide (2), while the Ethnographic Atlas documents cross-cultural variation across 1200 societies in traits such as marriage and inheritance rules, kinship and political structure, and religious beliefs (3, 4). While languages, religions and customs such as marriage certainly vary within societies, they typically characterize, and sometimes define, entire social groups. Given that societies differ, this inevitably generates between-group variation (5). Psychologists and economists have also documented variation between societies in cognition and economic norms (6–8), challenging earlier notions of a universal human psychology. Again, while there is much within-society variation in these measures, there is also clear between-society structure.

This behavioral variation is unlikely to have a genetic basis. While human populations do vary genetically (9), between-group genetic variation is orders of magnitude smaller than typical between-group behavioral variation (5). Behavioral variation is also not entirely determined by ecology. While ecology matters, cultural history is often a stronger predictor of human behavioral variation (10, 11). A substantial portion of between- and within-group human behavioral variation is therefore cultural, i.e. transmitted non-genetically via social learning from individual to individual within and across social boundaries.

Simultaneously, migration has been a constant fixture of our species for millenia. *Homo sapiens* migrated out of Africa in multiple waves beginning around 100kya (12), reaching South America by 14kya (13). Migration continued within and between global areas throughout prehistory (14, 15). At small scales, humans are unique among primates in that both males and females disperse to non-natal groups, creating genetically unrelated communities and facilitating the spread and recombination of ideas and customs (16). At large scales, migration has spread society-transforming traits such as agriculture (17) and horseback archery (18). In the modern era, improved transportation technologies such as steamships and aeroplanes have allowed unprecedented mass voluntary migrations. Mass migration transformed the USA in the early 20th century (19), while international migration increased in volume (number of migrants) and scope (diversity of destinations) in the last century (20).

In a sense, these two phenomena - extensive between-group cultural variation and frequent migration - are contradictory. It is well known in population genetics that even small amounts of migration can rapidly break down between-group genetic structure (21, 22). If migration acts on cultural variation in the same way as it acts on genetic variation, we would expect that the frequent migration noted above would rapidly destroy between-group cultural variation, resulting in a homogenous mass world culture. Of course, it does not act in the same way. Migrants are stuck with their genes, but they may change their cultural traits, and often do so within one or two generations. This process

of *acculturation*, defined as psychological or behavioral change resulting from migration (23), could, in principle, maintain between-group cultural variation even in the face of frequent migration.

A growing body of quantitative empirical research has examined migrant acculturation on various measures shown to vary cross-culturally (see Supplementary Material). Psychologists have tested migrants with non-Western heritage living in Western countries on measures shown to exhibit East-West differences, such as collectivism, social attribution, self-enhancement and self-esteem (24–26). Economists and political scientists have measured traits such as trust in institutions via large-scale surveys in multiple generations of migrants (27–29). These studies typically show that (i) acculturation is never complete in a single generation, with first generation migrants typically retaining some degree of heritage culture; and (ii) acculturation is nevertheless common, with second and subsequent generations shifting, sometimes substantially, towards the cultural values of the adopted society. For example, second generation British Bangladeshis have shifted around 50% towards local non-migrant values of collectivism and social attribution from their first generation parents' values (24). A study of four generations of migrants in the USA found that of 26 attitudes related to family, cooperation, morality, religion and government, 13 shifted 50% or more towards adopted country values between the first and second generation, and 23 had shifted 50% or more by the fourth generation (28). Another study estimated acculturation rates in second generation Tongan Americans at approximately zero for some traits and as high as 0.87 for others, with a mean of 0.39, where a value of 1 indicates complete assimilation (30).

While these studies confirm that acculturation occurs, and provide estimates of acculturation rates, they do not examine the individual-level dynamics (i.e. how migrants learn from others) that drive these population-level acculturation patterns, nor do they extrapolate from observed acculturation rates to long-term impacts on between-group cultural variation. Here I adapt population genetic models of migration to the cultural case to ask: (i) how strong does acculturation need to be, and what form should it take, in order to maintain different amounts of between-group cultural variation in the face of different levels of migration? (ii) are these levels of migration, acculturation and between-group cultural structure empirically plausible? I follow previous cultural evolution researchers (31, 32) in adapting population genetic methods, measures and concepts to analyse cultural change, on the assumption that genetic and cultural change are both systems of inherited variation (33). While previous cultural evolution models have examined the effect of migration on cultural diversity (31) and acculturation in specific migrant communities (30), no previous research has explicitly linked migration and acculturation to the maintenance of between-group cultural variation. Migration is frequently studied in economics (34), sociology (35), psychology (23) and cultural anthropology (36). While I draw on some of this empirical and theoretical work here, much of that research focuses on the proximate level (e.g. the lived experiences or psychological adjustment of migrants) and does not formally link individual-level migration and acculturation processes to population-level cultural dynamics.

These questions have relevance beyond academia. Migration and acculturation have always been

major factors in political and public discourse, and never more so than in today's increasingly interconnected world. As noted above, economic migration is at record global levels (20). The involuntary migration of refugees has also increased. The 'European migrant crisis' has seen unprecedented numbers of people crossing the Mediterranean from Syria and other conflict areas (37). As migration increases, public opposition to immigration often also rises (38). Much of this opposition reflects beliefs that immigrants are incapable of acculturating, and that migration will consequently weaken or destroy existing cultural traditions in receiving countries. For example, in the 2013 British Social Attitudes survey (39), 77% of respondents wanted immigration levels reduced, 45% said immigrants undermined Britain's cultural life (versus 35% who said they enriched it), and half agreed that one cannot be "truly British" unless one has British ancestry (51% agree) and shares British customs and values (50% agree). Politicians often appeal to such fears surrounding supposedly non-acculturating immigrants[1]. Debates of these issues in public and political spheres typically proceed with little empirical basis.

Here I present models exploring how migration and acculturation interact to maintain, reduce or eliminate between-group cultural variation. The models are simple, but can guide empirical research by highlighting what we can infer from current evidence, and what evidence is lacking. Model 1 explores how migration, acculturation and assortation affect between-group variation in functionally-neutral cultural traits. Model 2 examines how migration and acculturation affect a non-neutral cooperative trait that is individually costly but group beneficial. Models presented are recursion-based simulations tracking the frequency of cultural traits over time, written in R (40) and available at https://github.com/amesoudi/migrationmodels.

[1]For example, Marine Le Pen of the French *Front national* has said "Immigration is an organized replacement of our population. This threatens our very survival. We don't have the means to integrate those who are already here. The result is endless cultural conflict.". Geert Wilders of the Dutch *Party for Freedom* has said "[Muslim immigrants] bring along a culture that is not ours. Islam is not there to integrate; it's there to dominate.". Nigel Farage of the *UK Independence Party* has said "If we went to virtually every town up eastern England and spoke to people about how they felt their town or city had changed for the last 10 to 15 years, there is a deep level of discomfort. Because if you have immigration at these sort of levels, integration doesn't happen". Donald Trump was elected US President partly on an anti-immigrant platform, including building a wall to prevent Mexican immigration and a ban on immigrants from Muslim countries. It is not my aim here to take a stance on the normative and political issue of migration policy, only to scrutinize the logical and empirical claims inherent in such statements and policies, e.g. that immigrants can never acculturate (Le Pen), or that acculturation depends on the level of migration (Farage).

Model 1: Migration, acculturation and cultural diversity

I start with a simple model of migration borrowed from population genetics, Wright's island model (21, 22), to which I later add acculturation. Parameters are listed in Table 1. Assume a large population divided into s equally sized and partially isolated sub-populations. Consider a trait (originally an allele, but here a cultural trait) that has mean frequency across the entire population of $\bar{p}$. Every timestep, each individual migrates with probability m. Migration is random and simultaneous, such that a proportion m of individuals are randomly removed and this pool of migrants is randomly allocated across all newly-vacant spots in the entire population. Hence a proportion m of individuals in each sub-population will be immigrants, taken from a pool with trait frequency $\bar{p}$.

Table 1: Parameters in Model 1

Parameter	Definition
s	The number of sub-populations, and also the number of cultural traits.
p	The frequency of a trait in a sub-population
m	Migration rate: the probability in one timestep that an individual moves to a randomly chosen sub-population. Equivalently, the proportion of the population that moves in one timestep.
n	The number of demonstrators from whom individuals learn during acculturation.
a	Acculturation rate: the strength of conformist social learning, defined as the degree to which an individual is more likely to adopt the most-common trait among n demonstrators chosen from their sub-population, compared to unbiased, random copying.
r	Assortation strength. With probability $1 - r$, the n demonstrators are chosen at random. With probability r, sets of demonstrators all have the same cultural trait.

Consider a particular sub-population in which the frequency of the trait at time t is p. For a randomly chosen trait in this sub-population, the trait either came from a non-migrant in the previous timestep with probability $1 - m$, with the frequency among those non-migrants p_{t-1}, or from a migrant with probability m, with the frequency among those migrants being $\bar{p}$. The overall frequency is therefore (21, 22):

$$p = p_{t-1}(1 - m) + \bar{p}m \qquad (1)$$

We are interested in how migration breaks down, and acculturation prevents the breakdown, of between-group cultural variation. Assume therefore that initially there is complete between-group cultural variation, and no within-group variation. Consequently, assume s cultural traits, and at time

$t = 0$ all individuals in sub-population 1 have trait 1, all individuals in sub-population 2 have trait 2, and so on. To quantify the degree of population structure, I use Wright's F_{ST}, a measure typically used to quantify the degree of between-group genetic variation (21, 41), but recently used to quantify population structure in cultural traits (5). As a statistical measure, F_{ST} is neutral to transmission mechanism, and simply measures the probability that two randomly-chosen individuals from the same sub-population carry the same trait, compared to two randomly-chosen individuals from the entire population (see Supplementary Material). An F_{ST} of 1 indicates complete between-group variation and no within-group variation. An F_{ST} of 0 indicates no between-group variation, with all variation occurring within groups. In this model, at time $t = 0$, $F_{ST} = 1$, and we are interested in when this is maintained and when it drops.

It is difficult to obtain reliable real-world estimates of cultural F_{ST} given the lack of quantitative data in fields such as cultural anthropology. Moreover, while group differences are reported in sources like the Ethnographic Atlas (4), within-population variation is seldom measured. Cultural evolution researchers have begun to address this, finding a mean cultural F_{ST} of 0.08 for items on the World Values Survey (5) and 0.09 for a folktale (42). Another study lists F_{ST} values from 0.008 to 0.612 for various attitudes (43). Clearly between-group cultural variation can vary greatly per trait and population(s), but $F_{ST} = 0.1$ is perhaps a reasonable benchmark.

What is a plausible value of m? Migration rates differ across time periods and geographical scales. If a timestep in the model is taken as a biological generation, as it typically is in population genetics, then m is the probability that an individual migrates from their natal community during their lifetime. Lifetime migration rates have been estimated for several human populations within nation states (e.g. !Kung villages, or villages in Oxfordshire) at 0.1-0.33 (44). Another interpretation of m is the proportion of the population that are migrants. In the UK this has increased from 0.042 in 1951 (45) to 0.133 in 2015 (46). The USA has similar figures of 0.069 in 1950 and 0.134 in 2015 (47). A value of $m = 0.1$ is perhaps again a reasonable benchmark.

Following migration there is acculturation. While acculturation as a population level phenomenon certainly exists (see Supplementary Material), there is no research on the individual-level mechanisms by which an individual migrant alters their beliefs or practices as a result of learning from the wider community. The most plausible mechanism already modeled and tested in the cultural evolution literature is positive frequency-dependent bias, or conformity (32, 48–51). Conformity is defined as an increased tendency to adopt the most common trait among a sample of other individuals ('demonstrators'), relative to copying randomly. For example, if 70% of demonstrators are observed possessing trait A, then a conformist learner adopts trait A with a probability greater than 70%. An unbiased, non-conformist learner would adopt trait A with probability exactly 70%.

Evolutionary models show that conformity is likely to evolve in spatially variable environments and when individuals must choose between more than two traits (52), both features of the modified island model described above. Conformity has already been suggested as a mechanism that can maintain between-group cultural variation (49), although not as a mechanism of acculturation (e.g. in (49),

conformity occurs before migration and so does not affect migrants). Finally, there is evidence that people employ conformity from lab studies (48, 51, 53) and real-world data (54). Conformity is also found in non-human species when naive individuals must acquire equally-rewarded cultural traits in a spatially heterogeneous environment with migration (55), as modeled here.

Conformist acculturation is added to the island model in each timestep following the completion of all migration. It is assumed to apply to all individuals, not just new migrants. This allows acculturation to occur over multiple generations: if a new migrant does not switch traits immediately after migrating, they may do so in subsequent generations. It also parsimoniously assumes that the same conformist bias applies to all individuals, rather than positing special learning mechanisms for migrants and non-migrants.

Conformist acculturation is implemented following Boyd and Richerson (32), by assuming that individuals adopt traits based on their frequency among n randomly chosen demonstrators from their sub-population, with parameter a increasing the probability of adoption of the most frequent trait among those n demonstrators. When $a = 0$, transmission is unbiased and non-conformist. When $a = 1$ there is 100% probability of adopting the most frequent trait among the demonstrators, if there is one. Boyd and Richerson (32) modeled the case when $n = 3$ and there are two traits using binomial theorem. Here I extend their formulation to $n > 3$ and more than two traits using multinomial theorem.

If p_i is the frequency of trait i in the sub-population after migration (see Equation 1), then the frequency of trait i in that sub-population after conformist acculturation, p'_i, with n demonstrators and s traits, is given by:

$$p'_i = (1-r)\Bigg[\sum_{k_1,k_2,...k_s=n} \binom{n}{k_1, k_2, ...k_s} \prod_{j=1}^{s} (p_j^{k_j}) \cdot X_i\Bigg] + rp_i \tag{2}$$

The first part of Equation 2 gives the updated trait frequency arising from a fraction $1 - r$ of the sub-population that picks demonstrators at random. The expression in the square brackets contains the multinomial theorem and gives, for each combination of s traits among n demonstrators, the probability of that combination randomly forming and giving rise to trait i. $k_1, k_2...k_s$ represent all combinations of s non-negative integers from 0 to s such that the sum of all k is n. Conceptually, k_j represents the number of demonstrators who possess trait j. The multinomial coefficient gives the number of ways in which demonstrators with that combination of traits can form. This is multiplied by the probability of that combination forming, with each trait frequency p_j raised to the number of times that trait appears in the combination, k_j. This is multiplied by X_i, which gives the probability of adopting trait i for that combination of demonstrators. In cases where there is a single most-common trait, i.e. a single maximum k, k_{max}, in a combination, then:

$$X_i = \begin{cases} k_i/n + a(n-k_i)/n & \text{if } 0 < k_i < n \text{ and } k_i = k_{max} \\ k_i/n - ak_i/n & \text{if } 0 < k_i < n \text{ and } k_i \neq k_{max} \\ k_i/n & \text{otherwise} \end{cases} \tag{3}$$

Here, the conformity parameter a increases the probability with which the majority trait is adopted, and decreases the probability with which minority traits are adopted. When there is no single maximum value of k_i, transmission is always unbiased such that $X_i = k_i/n$. This covers combinations that have two joint-highest values of k.

The final part of Equation 2 deals with non-random demonstrator formation. It is reasonable to assume that, in reality, migrants are more likely to interact with other migrants, and non-migrants with other non-migrants. This is analogous to assortative mating in genetic evolution. In the model, I assume that a fraction r of demonstrators form such that only sets of culturally homogenous demonstrators come together. These form with probability equal to the frequency of the trait they all exhibit, p_i. Assortation therefore leaves cultural trait frequencies unchanged, hence the term rp_i.

The Supplementary Material gives an example of how Equations 2 and 3 yield trait frequencies following conformist acculturation and assortation. It was not possible to find an algebraic expression for F_{ST} in terms of m, n, a and r so the model was implemented using numerical simulation tracking trait frequencies in each sub-population over time. As an independent replication of the results, the model was also implemented as an individual-based model in which individuals and their traits are explicitly simulated, and which gave almost-identical results (see Supplementary Material).

Results

Migration without acculturation eliminates between-group variation

Without acculturation, migration always eliminates between-group variation, just as in Wright's original island model and specified by Equation 1. Figure 1 shows time series of F_{ST} for a low ($m = 0.01$) and high ($m = 0.1$) migration rate. In both cases, the grey $a = 0$ lines fall to zero. Each trait in each population converges on the mean frequency of that trait across the whole population. Because each sub-population is equally sized, and each trait starts out at unity in one of these s sub-populations, this mean frequency $\bar{p} = 1/s$ for every trait. This can occur rapidly: for $m = 0.01$, the perfect between-group structure completely disappears within 300 timesteps, while for the more plausible $m = 0.1$ it disappears within 30.

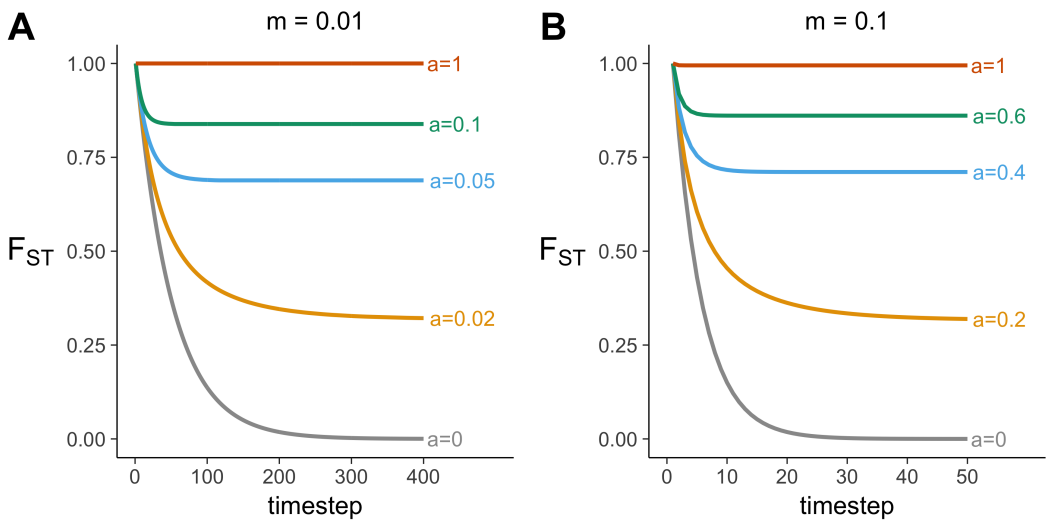

Figure 1: Time series showing changes in F_{ST} over time for (A) a low migration rate m=0.01 and (B) a high migration rate m=0.1, at varying strengths of acculturation, a. Other parameters: s=5, n=5, r=0.

Acculturation can maintain between-group cultural variation

Figure 1 shows that when there is complete acculturation ($a = 1$, red lines), then F_{ST} remains at 1, indicating the maintenance of complete between-group cultural variation. Values of a between 0 and 1 generate equilibrium values of F_{ST} between 0 and 1, at a level at which migration and acculturation balance out. That is, the decrease in a common trait's frequency as a result of migration is equal to the amount by which conformist acculturation increases the common trait's frequency after migration. Notably, even small amounts of acculturation can restore F_{ST} to realistically high values. In Figure 1, when $m = 0.01$, then $a = 0.1$, or a 10% chance of adopting majority traits per timestep, maintains F_{ST} at approximately 0.87, which is already higher than the highest F_{ST} found by (43). An average F_{ST} of approximately 0.35 can be maintained with just $a = 0.02$. When $m = 0.1$, then higher acculturation rates are needed to maintain between-group structure, but an a of just 0.2 is needed to maintain F_{ST} at realistic levels of around 0.35.

Figure 2 shows how the full range of a affects F_{ST}, for three different migration rates and four different values of n. Figure 2 confirms that higher F_{ST} can be maintained with stronger acculturation (larger a) and lower migration (smaller m). For high migration rates, equilibrium F_{ST} also increases with n. At low migration rates, $n = 3$ is just as effective as larger values of n. This is because the migration rate is so low as to maintain homogeneity in demonstrators no matter how small the sample.

The top row of Figure 3 shows how F_{ST} varies across the full m and a parameter space, for two different values of n. In each case, higher values of F_{ST} are maintained with stronger acculturation (higher a) and lower migration (smaller m). Increasing n from $n = 3$ (top left) to $n = 7$ (top right) increases the parameter space in which F_{ST} is maintained above zero. This is as expected. When

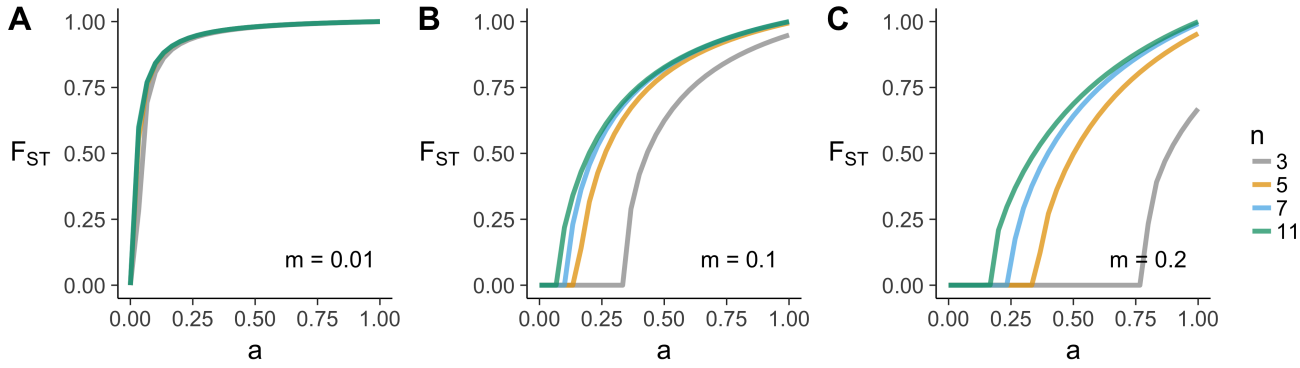

Figure 2: Equilibrium F_{ST} as a function of acculturation strength, a, at three different migration rates, m (panels A-C), and different numbers of demonstrators, n (colored lines). Other parameters: s=5, r=0; plotted are values after 500 timesteps.

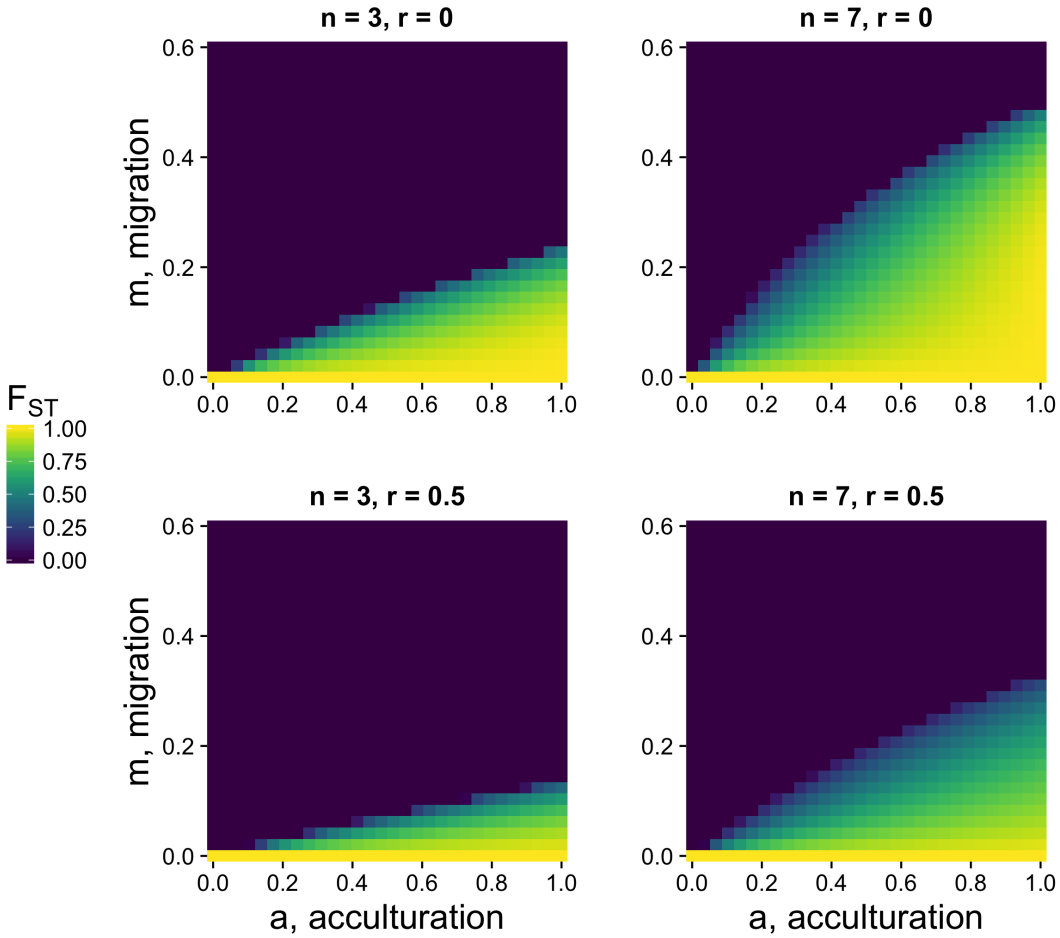

Figure 3: Heatmaps showing equilibrium F_{ST} for varying acculturation rates, a, and migration rates, m, separately for different values of n, the number of demonstrators, and r, the probability of assortation. Other parameters: s=5; plotted are values after 500 timesteps.

$n = 3$, there is little opportunity for conformity to act (only when two demonstrators exhibit one trait and one demonstrator exhibits another), while for $n = 7$ there are more opportunities (demonstrator trait ratios of 6:1, 5:2 and 4:3 all give majorities). For high migration rates of $m > 0.5$, no amount of acculturation can prevent the elimination of between-group cultural variation, although this level of migration is already unrealistically high. For plausible values of m around 0.1, a substantial range of a yields realistic F_{ST}s of 0.1 or more, especially when there are many demonstrators.

Assortation reduces the effect of acculturation

Assortation acts to restrict the parameter space within which F_{ST} is maintained, as shown in the lower two panels in Figure 3 where $r = 0.5$. This is as expected given Equation 2. Assortation counteracts the effect of conformity by reducing the likelihood that heterogeneous sets of demonstrators come together, which is required for conformity to operate.

Summary of Model 1

Model 1 affords the following insights. First, even small amounts of migration can rapidly break down between-group cultural variation. This is analogous to how migration in genetic evolution can rapidly break down between-group genetic variation, and is well known from population genetics. Second, even small amounts of acculturation can counteract this effect of migration and maintain plausible amounts of between-group cultural variation. This is unique to cultural evolution: migrants are stuck with their genes, but can change their cultural traits. Third, the modelling exercise reveals a paucity of empirical data on even these simple processes and measures, particularly quantitative estimates of the strength or form of acculturation. Nevertheless, given our best estimates of m and F_{ST} being quite low, only small amounts of acculturation are needed to maintain plausible amounts of between-group cultural variation. Existing acculturation research (see Supplementary Material) suggests that acculturation is easily strong enough to meet this criterion, although there is a need for more research along the lines of (30) that directly estimates a across multiple migrant generations, and tests whether it is conformist. Finally, assortation acts against acculturation: when individuals only learn from culturally homogenous sets of demonstrators, then acculturation has a weaker effect. This formalises the intuition that more integrated migrant minorities are more likely to acculturate than marginalized minorities.

Model 2: Migration, acculturation and cooperative behavior

Model 1 concerned the effects of migration and acculturation on neutral cultural variation: the cultural traits were equally likely to be copied and did not affect individuals' welfare or success. Migration was also random between groups. Much public concern over migration, however, centers on cooperative behavior and norms, for which neither of these assumptions are true. Think of concerns among some US citizens over Mexican immigration, and among some European citizens over North African or Middle Eastern immigrants. In such cases, people are concerned that migrants coming from societies with less-cooperative norms (e.g. high crime rates, high tax avoidance and corruption, military conflict, and weak or corrupt institutions) moving to societies with more-cooperative norms (e.g. low crime rates, low tax avoidance and corruption, or strong and stable institutions such as public health or education services) will bring their less-cooperative norms with them, free-ride on the more-cooperative norms of their adopted society, and cause a break-down of cooperation in the adopted society. Migration is not random here: people are more likely to move from less-cooperative to more-cooperative societies (56, 57), which will exacerbate the potential degradation of cooperation in the latter. This situation again concerns acculturation. The above scenario assumes that migrants bring and retain their non-cooperative norms with them, rather than acculturate to the cooperative norms of the adopted country.

Human cooperation is also of major scientific interest, with much debate concerning how to explain the unusually high levels of non-kin-directed altruism in humans (43, 58, 59). Typically, migration is seen as a force acting against the maintenance of cooperation because it breaks up groups of cooperators and spreads selfish free-riding behavior (58, 60). Theories of cultural group selection require stable between-group cultural variation in cooperative behavior and so need some acculturating mechanism to work against migration (43, 61).

Model 2 therefore examines the effect of migration and acculturation on the maintenance of a cooperative cultural trait in the face of incoming migrants with non-cooperative norms. Additional parameters used in Model 2 are listed in Table 2.

Table 2: Additional parameters in Model 2

Parameter	Definition
N	Fixed number of individuals in the focal sub-population
p	Proportion of individuals in the focal sub-population who are cooperators
b	Benefit to the sub-population from each cooperator
c	Cost of cooperation borne by each cooperator
u	Cost of punishment borne by each cooperator, weighted by the proportion of defectors in the sub-population
v	Punishment penalty borne by each defector, weighted by the proportion of cooperators in the sub-population
L	Strength of payoff-biased social learning within the sub-population

Individuals are either cooperators or defectors, and are in sub-populations of constant and equal size N. We are interested in the maintenance of cooperation in a sub-population where cooperation is common yet faces migrants coming from sub-populations where defection is common. Assume for simplicity a single focal sub-population initially composed entirely of cooperators ($p = 1$, where p is the proportion of cooperators), surrounded by a much larger meta-population that supplies defecting migrants and which is so large as to have a fixed $p = 0$.

Within the focal sub-population, each timestep each cooperator pays a cost c ($c > 0$) to benefit the entire sub-population by an amount b, where $b > c$. Defectors pay no cost and give no benefit. The total group benefit in the sub-population, bNp, is divided equally among all N sub-population members. Cooperators in the sub-population therefore have fitness $w_c = 1 + bp - c$ and defectors have fitness $w_d = 1 + bp$, where 1 is baseline fitness.

Here defectors will always have higher fitness than cooperators for $c > 0$ and always go to fixation, assuming some selective force such as payoff-biased social learning (see below) or natural selection. As soon as mutation, errors or migration introduce defectors into the cooperating group, cooperation will disappear. This is unrealistic for most human groups and makes the present model uninteresting. I therefore introduce a mechanism to maintain cooperation: coordinated altruistic (i.e. costly) punishment. Punishment is a common strategy for maintaining cooperation, and may arise via gradual trial-and-error to create institutions (62), conformity (63), between-group selection (58, 64) or other mechanisms. I am not concerned here with these processes, and assume that punishment has already evolved.

Hence, assume each cooperator pays a cost u/N per defector to reduce the payoff of each defector by v/N, where $v > u$ (58). There are Np cooperators who punish each defector, so defectors now have overall fitness of $w_d = 1 + bp - vp$. Each cooperator punishes $N(1 - p)$ defectors, so cooperators have fitness $w_c = 1 + bp - c - u(1 - p)$. Cooperators and defectors will have equal fitness when $w_d = w_c$, or when $p = p^*$, where

$$p^* = \frac{(c+u)}{(v+u)} \tag{4}$$

Defectors will invade a population of cooperators when $p < p^*$. That is, cooperation is maintained when cooperators are common enough that the punishment costs to defectors outweigh the costs of cooperating to cooperators. When $c > v$, cooperation is never maintained. Note that non-punishing cooperators could invade a population of punishing cooperators because the former would not pay the cost u. I assume that this second-order free-riding problem is already solved (e.g. by the mechanisms specified above) and non-punishing cooperators are not included in the model. I also assume that a sub-population entirely composed of defectors ($p = 0$) always has lower fitness than a sub-population with any cooperators ($p > 0$). See Supplementary Material for fitness plots and further details.

As in Model 1, the first timestep event is migration determined by migration rate m, but this is now payoff-biased. Individuals move to sub-populations with higher mean fitness than their own and at a rate proportional to the mean fitness difference between their own sub-population and the wider meta-population (56). By assumption, in Model 2 this will always involve defectors coming into the sub-population and replacing cooperators (who are assumed to die or migrate out themselves) at a rate proportional to $W - 1$, where W is the mean fitness of the focal sub-population and 1 is the mean fitness of the meta-population where $p = 0$. The frequency of cooperators in the sub-population after migration, p', is therefore

$$p' = p(1 - m\mu(W - 1)) \tag{5}$$

The constant μ ensures that $m\mu(W-1)$ never exceeds m, so that m is always the maximum migration rate. Equation 5 resembles Equation 1, but with m now a function of relative sub-population fitness, and $\bar{p} = 0$.

Following migration there is acculturation, identical to Model 1. With probability a, each individual adopts the most common strategy (cooperate or defect) amongst n demonstrators in their sub-population according to Equation 2 (with $s = 2$, given two traits, cooperate and defect). This occurs after all migration has finished.

Finally there is payoff-biased social learning within each sub-population. With probability L, individuals switch strategies in proportion to the fitness payoff difference within their sub-population between the alternative strategy and their current strategy. If p' is the frequency of cooperators after migration and conformist acculturation, then the frequency after payoff-biased social learning, p'', is given by:

$$p'' = p' + Lp'(1 - p')(w_c - w_d)\gamma \tag{6}$$

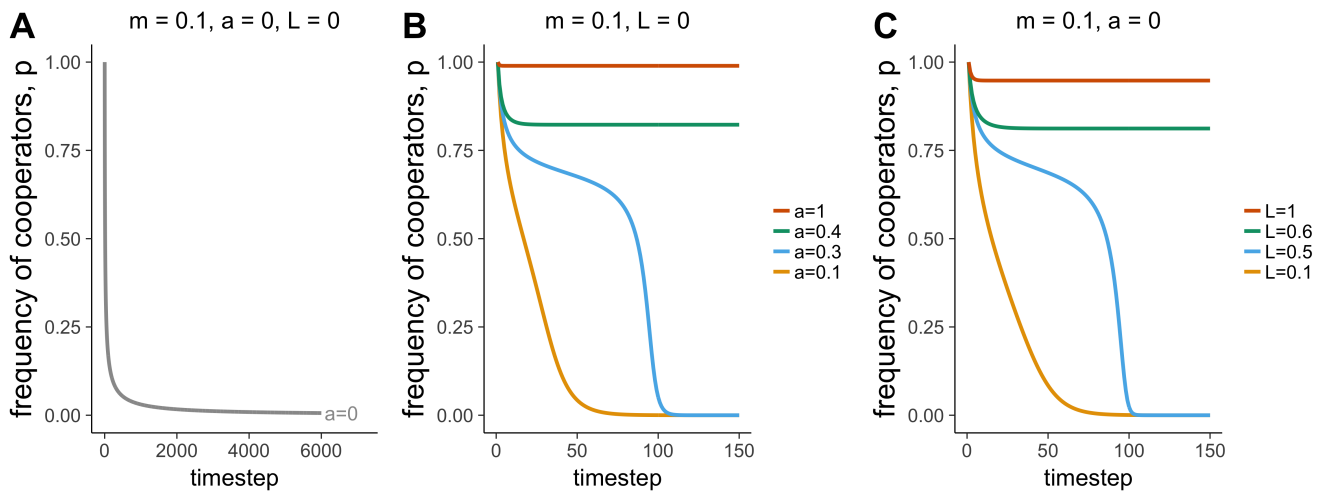

Figure 4: Time series showing changes in p over time in the face of payoff-biased migration (m=0.1), (A) in the absence of acculturation (a=0) and payoff-biased social learning (L=0); (B) at varying strengths of acculturation, a, and (C) at varying strengths of payoff-biased social learning, L. Other parameters: n=5, r=0, b=1, c=0.2, u=0.1, v=0.5.

where γ is a constant that scales L according to the maximum possible fitness difference. Payoff-biased social learning creates a selective force within the sub-population favoring whichever strategy gives the highest payoff, which in turn depends on Equation 4.

Model 2 comprises cycles of Equations 5, 2 and 6 (payoff-biased migration, conformist acculturation and payoff-biased social learning). As we are interested in the maintenance of cooperation, we track the proportion of cooperators p over time in the focal sub-population which initially comprises all cooperators.

Results

Payoff-biased migration alone eliminates cooperation

In the absence of acculturation ($a = 0$) and payoff-biased social learning ($L = 0$), payoff-biased migration (m>0) causes defectors to flow from the all-defect meta-population into the initially all-cooperate sub-population to eliminate cooperation entirely (Figure 4A). Because the strength of payoff-biased migration is a function of the mean population fitness relative to the mean fitness of the metapopulation, the rate of decline is initially fast due to the high initial mean fitness of the cooperative sub-population, and slows as cooperators leave and mean fitness drops.

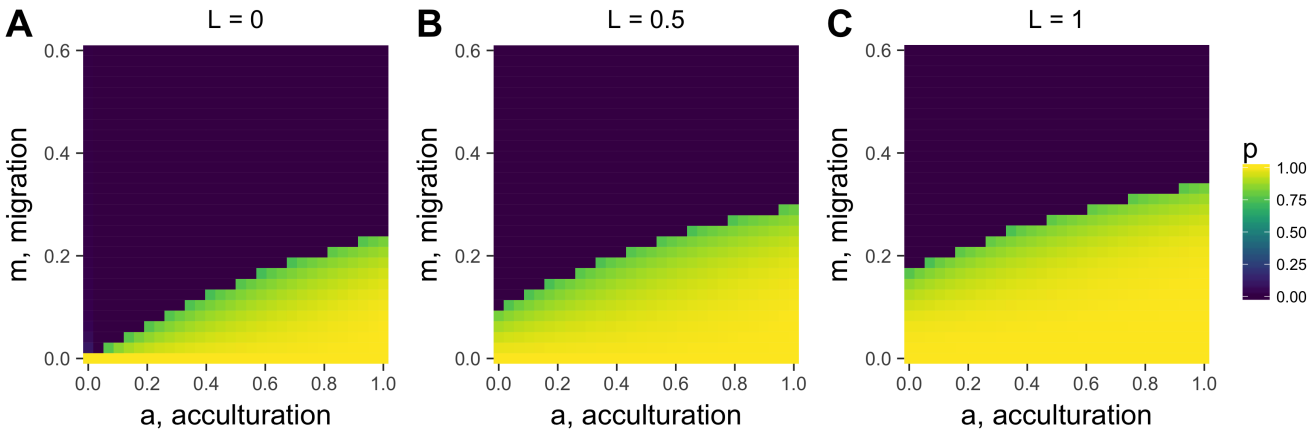

Figure 5: Heatmaps showing equilibrium p for varying acculturation rates, a, and migration rates, m, separately for different values of L, the strength of payoff-biased social learning. Other parameters: r=0, n=5, b=1, c=0.2, u=0.1, v=0.5; plotted are values after 1000 timesteps.

Conformist acculturation can maintain cooperation

As in Model 1, when conformist acculturation is sufficiently strong (i.e. a and n are sufficiently large), then the decline in cooperation is halted and cooperation is maintained at a point where acculturation and migration balance out (Figure 4B). This can also be seen in Figure 5A, which shows a similar relationship between a and m as in Model 1: cooperation is most likely to be maintained when a is high, and m is low.

Two points are worth noting. First, when acculturation is not strong enough to maintain cooperation, it actually speeds up the decline. Compare the several thousand timesteps it takes for cooperation to drop to approximately $p = 0$ in Figure 4A with $a = 0$ to the 100 timesteps it takes to reach $p = 0$ in Figure 4B with $a = 0.1$. Conformity favours the majority trait, which when $p < 0.5$ is defection, speeding up the convergence on $p = 0$.

Second, unlike in Model 1, we see an interesting dynamic at values of a that are not quite strong enough to maintain cooperation (e.g. $a = 0.3$ in Figure 4B). An initial rapid decline in cooperation when $p = 1$ slows as p declines, then increases again. This can be understood in terms of the relative strengths of payoff-biased migration and conformist acculturation. Payoff-biased migration is strongest at $p = 1$ and weakens as it approaches its stable equilibrium at $p = 0$. Conformist acculturation has an unstable equilibrium at $p = 0.5$ where the two traits are equal in frequency, and increases in strength as the frequency approaches the stable equilibria at $p = 0$ and $p = 1$. In Figure 4B when $a = 0.3$, the initial rapid decline is due to strong payoff-biased migration near $p = 1$. As p decreases, payoff-biased migration weakens and conformist acculturation slows the decline. As we approach $p = 0.5$ conformity weakens, allowing payoff-biased migration to take over and increase the rate of decline. When p drops below 0.5, conformity starts to work with payoff-biased migration to increase the rate of decline further.

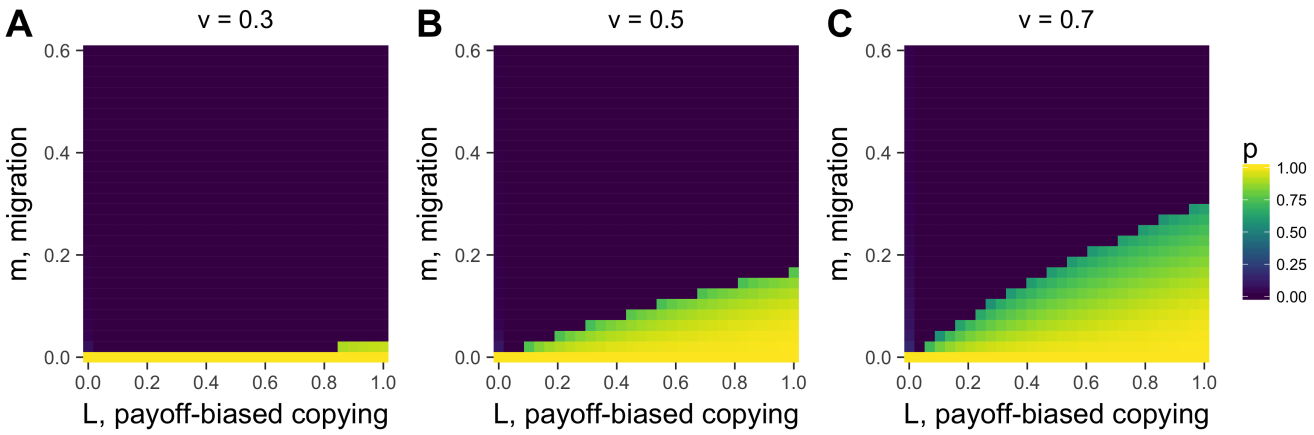

Figure 6: Heatmaps showing equilibrium p for varying strength of payoff-biased within-group social learning, L, and migration rates, m, separately for different values of v, the punishment costs to defectors. Other parameters: r=0, a=0, b=1, c=0.2, u=0.1; plotted are values after 1000 timesteps.

This dynamic means that there are fewer values of a in Model 2 at which p is maintained at intermediate values, compared to Model 1. This can be seen in Figure 5A: final frequencies are typically either $p = 0$ (dark blue) or $p = 1$ (yellow), with little in between. Contrast this to Model 1 in Figure 3, which features more intermediate (green) frequencies.

Payoff-biased social learning acts like an acculturating mechanism

Figure 4C shows a strikingly similar dynamic for payoff-biased social learning (L) as for conformist acculturation. When L is large, cooperation is maintained. When L is small, cooperation declines to zero, with a similar-shaped curve for intermediate values of L. Payoff-biased social learning therefore acts as an acculturating mechanism, like conformity. It does this because cooperation is favoured when common, and disfavoured when less common, similar to conformity (see Supplementary Material). Figure 5B and 5C show how L increases the parameter space in which a maintains cooperation in the face of migration, confirming that they work in the same manner.

However, whereas conformist acculturation has an unstable equilibrium at $p = 0.5$ (given that there are two traits), payoff-biased social learning has an unstable equilibrium at p^*. In Figure 4C $p^* = 0.5$, so there is little difference to Figure 4B. However, at different values of p^*, there will be different dynamics. Figure 6 shows how changing the basin of attraction for cooperation via the punishment penalty for defectors, v, and therefore p^* (via Equation 4), alters the effect of L. When v is small, p^* is large, cooperation has a smaller basin of attraction, and L mostly favours defectors. When v is large, p^* is small, cooperation has a larger basin of attraction, and L largely favours cooperators. Conformist acculturation, by contrast, does not vary with v or any other fitness parameter, as it solely works on the basis of trait frequency.

Summary of Model 2

Like Model 1, Model 2 showed that conformist acculturation works to maintain cultural traditions in the face of migration. Rather than neutral cultural variation, here the tradition involves cooperative behavior that is lost due to payoff-biased migration bringing non-cooperators from low-payoff to high-payoff sub-populations. The evidence reviewed in the Supplementary Material includes cases of acculturation of cooperative behavior, with migrants from low-trust countries acculturating to the high-trust norms of their adopted country within a few generations (27). More empirical work is required to accurately specify acculturation rates across a broader range of societies and norms, and test whether it is conformist. However, we can apply the same insight here as from Model 1: surprisingly little acculturation is needed to maintain cooperation in the face of realistic levels of migration. Figure 5A, for example, shows that for $m = 0.1$, an a of around 0.3 (with $n = 5$) is sufficient to maintain cooperation.

On the other hand, where migration *is* strong enough to allow non-cooperating migrants to increase in frequency, conformity actually speeds up the loss of cooperation when cooperation becomes a minority trait. There are also fewer intermediate cases: cooperation is either maintained at a high level, or lost completely.

Finally, within-group payoff-biased social learning acts like an acculturating process, also maintaining cooperation in the face of migration. This is because cooperation is frequency dependent, with cooperators having high fitness when common due to the presence of punishment. Unlike conformity, the acculturating power of payoff-biased social learning depends on the fitness functions and the strength of punishment, which in reality may represent the strength of sanctioning institutions. In particular, when punishment of defectors is more effective via higher v (stronger sanctioning institutions), then payoff-biased social learning more effectively prevents migration from eliminating cooperation.

Discussion

Public debates concerning migration often proceed with little empirical basis. Academic research into migration is voluminous but seldom seeks to formally link individual-level learning, interaction and acculturation to population-level patterns of cultural diversity and change. I have attempted here to formalise the processes that contribute to the maintainenance and loss of cultural diversity in the face of migration. Migration itself (m) breaks down between-group cultural variation and homogenises behavior. Acculturation, here assumed to be conformist, prevents this breakdown. This acculturation effect increases with both the strength of the conformist learning bias (a) and the number of individuals from whom one learns (n), but weakens when individuals interact assortatively with culturally similar others (r). Model 1 found that surprisingly little acculturation is needed in order to maintain between-group variation in functionally neutral cultural traits given realistic rates of migration. Model 2 found similar results for a cooperative cultural trait, which is additionally subject to fitness costs and benefits. Even though payoff-biased migration acts to reduce cooperation, conformist acculturation and/or payoff-biased social learning (the latter working with sanctioning institutions that punish non-cooperators) can preserve cooperation.

How do these insights relate to the empirical data concerning migration and acculturation? The evidence regarding the strength of acculturation reviewed in the Supplementary Material suggests that migrants often shift around 50% towards the values of their adopted society every generation, although this varies across traits and societies. In the context of the models, we can tentatively conclude that these acculturation rates are easily strong enough to maintain cultural traditions in the face of migration. The models suggest that values of a much less than 0.5 can preserve variation for realistic values of m. If this is the case, then common fears that migration will inevitably destroy existing cultural traditions are likely to be exagerated or unfounded. Yet this is only a very loose comparison. There is little quantitative work that tries to measure acculturation rates in a way comparable to acculturation as modelled here. We do not know how migrants integrate social information from multiple sources, whether they do this in a conformist manner, the size and diversity of their social networks, or how this changes with successive generations who experience different social environments from their parents. Perhaps demonstrator-based biases, where people preferentially learn from certain sources such as parents, teachers or celebrities, are more appropriate learning mechanisms (32). We also do not know whether acculturation of cooperative norms is driven by conformist or payoff-biased social learning, both of which have similar acculturating effects but for different reasons.

The models presented here necessarily comprise many simplifying assumptions and omissions that could be addressed in future models. The present models failed to incorporate any benefits of migration, such as when migrants bring beneficial new skills and knowledge into a society and subsequently recombine them with existing skills and knowledge. The assumption of Model 2 that migrants always possess non-cooperative norms is obviously unrealistic. Future models might

examine the two-way exchange of cooperative behavior between multiple sub-populations, and the consequences for between-group competition by allowing N to vary as a function of mean sub-population fitness (56). The present models only allowed individuals to hold one trait at a time. Future models might examine the simultaneous acculturation of different traits at different rates, as found empirically (30), and the consequences for multi-dimensional cultural diversity. The traits here are discrete whereas many cross-cultural measures are continuous, which may gradually shift over time due to averaging across different demonstrators (32).

Migration is one of the fundamental drivers of genetic evolutionary change, along with selection, mutation and drift. Migration is surely also a fundamental factor within cultural evolution, yet works differently due to the often-rapid acculturation of migrants to local behavior. A major scientific and applied challenge for cultural evolution research is to explore the role of migration and acculturation in shaping human cultural diversity both past and present. The models here provide a first step towards this goal, but also highlight major gaps in our empirical knowledge regarding how acculturation operates at the individual-level, which is crucial for anticipating the population-level consequences of migration on cultural change and variation.

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Supplementary Material for 'Migration, acculturation, and the maintenance of between-group cultural variation'

Alex Mesoudi *

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

1 Evidence for migrant acculturation

There is a growing literature in economics, sociology and psychology that compares quantitative measures of behavioral or psychological traits across multiple generations of immigrants. This work aims to determine whether immigrants (or their descendants) retain the trait values of their country of birth or shift towards the trait values of their adopted country, in those cases where the two are different. If there is a shift, studies often determine its magnitude, how it varies with different combinations of adopted and birth countries, how it varies with age of migration (for first generation migrants), and how it persists over subsequent generations (second, third etc. generations). Using standard terminology, first generation migrants are defined as those born and raised in one country and who moved to another country after the age of 14, second generation migrants are children of first generation migrants, third generation are children of second generation, and so on.

Note that acculturation as considered in this empirical literature, as well as in the models in the current study, is considered in the restricted sense of the extent to which migrants become more similar to the adopted population, or retain their heritage values, on a single quantitative dimension. This is clearly only one possible acculturation dynamic. In Berry's (1) classification of acculturation styles, this is the *assimilation* vs *separation* dimension, the former involving shifts in migrants towards host values, the latter involving retention of heritage values. Berry (1) also highlights the possibility of *integration*, which entails maintaining heritage traits *and* adopting host society traits and possibly merging the two; and *marginalization*, which entails the rejection of both heritage and host society traits. Similarly, political scientists categorize modern nation state policies on migration as *exclusionary*, *assimilationist* or *multicultural* (2). The *integration* and *multicultural* dynamics in these schemes serve to highlight how migrants can contribute to and shape their adopted country's culture, not just accept or reject it; in other words, acculturation can involve changes in non-migrants due to the influence of migrants. Migration is a hugely complex phenomenon, but the empirical literature reviewed here, and the models in this study, represent an attempt to understand one particular simplified aspect of this complex reality.

Table S1 presents some example findings from the economics, sociology and psychology literatures, where mean values from multiple migrant generations are reported. It is necessarily selective, but

broadly representative of other studies (3–5). From Table S1, and those other studies, we can make the following empirical generalizations which inform the models in the current study:

- **Complete one-generation assimilation is rare.** It does not appear that first generation migrants acculturate/assimilate completely to their adopted country's values. Table S1 shows several traits for which first generation migrants differ from non-migrants, often substantially, and in the direction predicted by the cross-cultural research mentioned in the main text (6, 7). For example, (8) found that first generation British Bangladeshi migrants are more collectivistic and show more situational, and less dispositional, social attribution compared to White British non-migrants. This reflects findings in cross-cultural psychology that Western societies are less collectivistic, and show more dispositional and less situational attribution, than non-Western societies (9). Similarly, (10) found that non-Western first generation migrants to high trust countries such as Denmark, Norway and Sweden show much less trust, again in line with existing cross-cultural research. While there may be other traits not shown in Table S1 that do show complete within-generation assimilation, this seems rare. A wealth of literature shows that cultural history is important, and people are shaped by the values they acquire during childhood and early life (4, 5).

- **Acculturation is common and occurs over multiple generations.** While no trait in Table S1 shows one-generation assimilation, virtually all traits show some degree of gradual acculturation. First generation migrants often show a partial shift towards their adopted country's values, and second and further generations show shifts that are as large or larger. In many cases this shift is quite substantial, with second generation migrants sometimes moving more than 50% of the way towards non-migrant values from their first generation parents' or heritage country's values. In other cases shifts are only evident after multiple generations. In a rare study of four generations of migrants living in the USA, (4) found that of 26 attitudes related to family, cooperation, morality, religion and government, 13 attitudes showed a shift of 50% or more towards adopted country values between the first and second generation, and 23 had shifted 50% or more by the fourth generation.

- **Acculturation rates vary across traits.** In the same population, some traits can shift substantially while others show little change. For example, (8) found little difference between

first and second generation British Bangladeshis in religiosity and family contact, but a substantial shift in psychological traits such as collectivism or attributional style (Table S1). Similarly, (3) estimated acculturation rates (α in that paper) in US-born Tongan Americans (i.e. second generation migrants) at approximately zero for some traits (e.g. sibling adoption) and as high as 0.87 for others (e.g. ranking of family lines). (4) found that trust-related attitudes show stronger acculturation than family and moral values.

In terms of the models presented in this study, the above empirical generalizations tell us that (i) an acculturation rate of $a = 1$ is implausible, given that complete one-generation assimilation is rarely if ever observed, (ii) acculturation occurs over multiple generations, justifying our modelling assumption that a applies to all individuals and not just new migrants; and (iii) the range of F_{ST}s documented in the literature and generated in the model may be the product of different a rates applying to different traits. Furthermore, the variation across traits justifies our treating cooperative traits (Model 2) as different to neutral traits (Model 1). It is interesting to note that trust-based cooperative traits measured by (4) showed the most rapid acculturation.

Table S1: Empirical patterns of acculturation. For most measures, migrants are intermediate between heritage and host values (where available), and/or 2nd generation migrants are closer to host values than 1st generation migrants. Either of these indicate acculturation.

Trait	Host country	2nd generation	1st generation	Heritage country	Reference
Collectivism	UK: 5.45 (sd=0.77, n=99)	5.93 (sd=0.66, n=79)	6.29 (sd=0.57, n=108)	Bangladesh: NA	(8)
Dispositional attribution	UK: 5.27 (sd=0.88, n=99)	5.14 (sd=0.79, n=79)	4.94 (sd=1.01, n=108)	Bangladesh: NA	(8)
Situational attribution	UK: 4.38 (sd=1.01, n=99)	4.87 (sd=1.04, n=79)	5.16 (sd=1.08, n=108)	Bangladesh: NA	(8)
Religiosity	UK: 1.86 (sd=1.21, n=99)	4.10 (sd=1.44, n=79)	4.83 (sd=1.34, n=108)	Bangladesh: NA	(8)
Family contact	UK: 3.09 (sd=2.44, n=99)	7.11 (sd=4.83, n=79)	7.33 (sd=5.23, n=108)	Bangladesh: NA	(8)
Self-serving bias	Canada: 0.36 (sd=0.65, n=98)	0.22 (sd=0.79, n=111)	NA	Japan: -0.67 (sd=1.05, n=222)	(11)
Self-esteem	USA: 5.36 (sd=0.93, n=166)	4.86 (sd=1.07, n=195)	NA	China: 4.72 (sd=0.96, n=153)	(12)
Dialectic self-perception	USA: 3.61 (sd=0.83, n=115)	3.89 (sd=0.65, n=129)	NA	China: 3.98 (sd=0.69, n=153)	(12)
Neuroticism	Canada: 49.9 (n=314)	52.0 (n=112)	52.2 (n=207)	China: NA	(13)
Extroversion	Canada: 49.0 (n=314)	46.2 (n=112)	42.45 (n=207)	China: NA	(13)
Openness	Canada: 53.5 (n=314)	52 (n=112)	45.65 (n=207)	China: NA	(13)
Agreeableness	Canada: 50.0 (n=314)	53.0 (n=112)	46.85 (n=207)	China: NA	(13)
Conscientiousness	Canada: 49.0 (n=314)	48.1 (n=112)	46.45 (n=207)	China: NA	(13)
Trust	Denmark: 6.80 (n=2616)	6.10 (n=35)	5.86 (n=73)	Outside Western Europe: NA	(10)
Trust	Norway: 6.61 (n=3088)	6.31 (n=17)	6.07 (n=73)	Outside Western Europe: NA	(10)
Trust	Sweden: 6.29 (n=3119)	6.01 (n=63)	5.43 (n=204)	Outside Western Europe: NA	(10)

Trait	Host country	2nd generation	1st generation	Heritage country	Reference
Trust	Switzerland: 5.99 (n=2686)	5.73 (n=82)	5.54 (n=258)	Outside Western Europe: NA	(10)
Trust	Netherlands: 5.83 (n=3167)	5.58 (n=126)	5.45 (n=244)	Outside Western Europe: NA	(10)
Trust	Austria: 5.48 (n=3783)	5.10 (n=221)	4.98 (n=192)	Outside Western Europe: NA	(10)
Trust	Belgium: 5.11 (n=2909)	4.46 (n=99)	4.71 (n=125)	Outside Western Europe: NA	(10)
Trust	France: 4.94 (n=3026)	4.75 (n=194)	4.72 (n=189)	Outside Western Europe: NA	(10)
Trust	Greece: 3.49 (n=1975)	3.69 (n=169)	4.27 (n=175)	Outside Western Europe: NA	(10)

Notes For all rows, 1st generation were born in the heritage country and moved to the host country after the age of 14. 2nd generation were born in the host country to 1st generation parents. Measures are only shown if there was a statistically significant difference between either host and heritage or host and 1st generation values (otherwise there would be no scope for acculturation in the 2nd generation). Collectivism, attribution & religiosity range from 1-7. Family contact is number of family members one sees in person in an average week. Self-serving bias is the "difference between the extent to which participants viewed... positively valenced traits to be characteristic of (a) themselves and (b) their same-sex peers", where the individual ratings ranged from 1-8. Self-esteem and dialectic self-perception range from 1-7. For self-serving bias, self-esteem and self-perception, the study authors report 'Asian Americans' without specifying generation; these are assumed to be 2nd generation, but could include some 1st generation. Big Five personality measures are standardized T scores based on North American college-age norms, with the mean set to 50 and 10 units indicating one standard deviation. 1st generation personality measures are the means of recent and early migrants given in the cited paper. For Trust values from (10), values are from the European Social Survey 2004-2007 and on a scale of 0-10.

2 Calculation of F_{ST}

Wright's F_{ST} is the proportion of total population variation that occurs between sub-populations rather than within. In our models we have a population divided into s equally-sized sub-populations and s different traits. To calculate F_{ST} we first calculate the total variance, i.e. the probability that two randomly chosen individuals from the entire population have the same trait, ignoring sub-population structure. If $X_{i,j}$ is the frequency of trait i in sub-population j, and $\bar{X}_i$ is the mean frequency of trait i across all sub-populations, then the total variance, var_{total}, is given by

$$var_{total} = 1 - \sum_{i=1}^{i=s} \bar{X}_i^{\,2}$$

We then calculate the within-group variance for each sub-population, i.e. the probability that two randomly chosen individuals from that sub-population have the same trait. If var_j is the variance in sub-population j, given by

$$var_j = 1 - \sum_{i=1}^{i=s} X_{i,j}^2$$

then the overall within-population variance, var_{within}, is the mean of these variances:

$$var_{within} = \frac{\sum_{j=1}^{j=s} var_j}{s}$$

F_{ST} is then given by

$$F_{ST} = \frac{var_{total} - var_{within}}{var_{total}}$$

3 Conformity for more than two traits and more than three demonstrators

Boyd and Richerson (14) provide a model for the change in trait frequency under the assumption of conformist transmission, such that traits that are more frequent are more likely to be adopted relative to unbiased transmission. Their basic model (on p.208) assumed two traits (c and d) and three demonstrators (they call these 'models' but this is confusing, so I use 'demonstrators'). They use the binomial theorem to calculate the probability that different sets of three demonstrators would meet at random and pass on their traits. A parameter D, equivalent to a in the current models so henceforth labelled a, specified the increased probability of adopting the majority trait (held by 2/3 of the demonstrators) and decreased probability of adopting the minority trait (held by 1/3 of the demonstrators), when demonstrators possessed different traits. When $a = 1$ there is maximum conformity, when $a = 0$ there is no conformity and transmission is unbiased. For two traits and three demonstrators, the frequency p' of a trait after conformity is given by

$$p' = p + ap(1 - p)(2p - 1) \qquad (S1)$$

where p is the frequency of the trait before conformity. This however only applies when there are three randomly chosen demonstrators and two traits. The effect of increasing a can be seen in Figure S1. Increasing a from 0.5 to 1 increases the speed with which the initially more common trait goes to fixation.

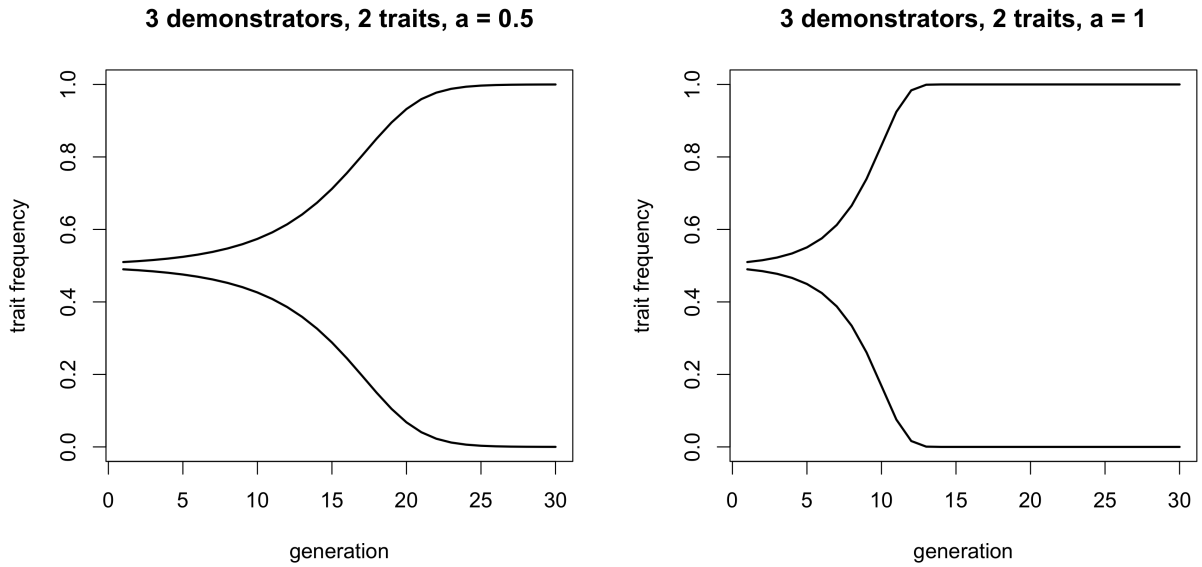

Figure S1: The effect of conformity on trait frequencies, for two traits and three demonstrators. The trait that is initially more common (initial frequency = 0.51) than the other trait (initial frequency = 0.49) goes to fixation. This occurs faster when the strength of conformity, *a*, is larger.

Boyd and Richerson (14) extended their model to include more than three demonstrators, but their formulation (p.213) failed to specify a conformity function. Efferson et al. (15) provided a clearer model of conformity with more than three demonstrators, also using the binomial theorem, showing that the effect of conformity increases with the number of demonstrators. However they did not extend to more than two traits. Nakahashi et al. (16) devised a model extending conformity to more than two traits, but used a different formulation to the binomial model. Their model used a parameter also labelled a: when their $a = 1$ there is no conformity, when their $a > 1$ there is conformity, and when their $a = \infty$ there is maximum conformity. However, this model has an unclear individual level interpretation. Boyd and Richerson's (14) conformity parameter has a clear meaning: when their parameter equals 1, then individuals faced with majority and minority traits always pick the majority trait. It is unclear, however, what Nakahashi et al's (16) $a = \infty$ means in this context, particularly when one wants to generate empirically testable predictions regarding acculturation strengths and compare to an individual-based model.

Here I use multinomial theorem to extend Boyd and Richerson's (14) model to more than three demonstrators and more than two traits, and with an interpretable conformity parameter.

If p_i is the frequency of a trait in the population, then to obtain the frequency of that trait in the next generation, p'_i, after conformist transmission with n randomly forming demonstrators and s traits, we can use the multinomial theorem:

$$p'_i = \sum_{k_1,k_2,...k_s=n} \binom{n}{k_1, k_2, ...k_s} \prod_{j=1}^{s} (p_j^{k_j}) \cdot X_i \qquad (S2)$$

where $k_1, k_2...k_s$ represent all combinations of s non-negative integers such that the sum of all k values is n. For example, when $s = 2$ and $n = 3$, then there are two k values, k_1 and k_2, and four combinations of k_1 and k_2 that sum to $n = 3$: $k_1 = 3$ and $k_2 = 0$; $k_1 = 2$ and $k_2 = 1$; $k_1 = 1$ and $k_2 = 2$; and $k_1 = 0$ and $k_2 = 3$. At the moment we assume that demonstrator formation is random. X_i specifies the probability of adoption of trait i for that set of k values, and incorporates the conformity parameter a. In cases where there is a single maximum k, k_{max}, in a combination, then:

$$X_i = \begin{cases} k_i/n + a(n - k_i)/n & \text{if } 0 < k_i < n \text{ and } k_i = k_{max} \\ k_i/n - ak_i/n & \text{if } 0 < k_i < n \text{ and } k_i \neq k_{max} \\ k_i/n & \text{otherwise} \end{cases}$$

Where there is no single maximum value of k_i, then transmission is always unbiased such that $X_i = k_i/n$.

To see how these equations work, Table S2 shows how to calculate the frequency p'_1 of trait $i = 1$ following conformity given two traits, 1 and 2 ($s = 2$) and three demonstrators ($n = 3$). The first three columns 'Dem 1-3' contain all possible combinations of traits 1 and 2 among the three demonstrators. k_1 and k_2 are the number of copies of trait 1 and 2 respectively in that row's demonstrators. 'Coef' contains the number of each combination of demonstrator traits ignoring order, and is the multinomial coefficient. The column $P(forming)$ gives the probability of that combination of demonstrators forming. This is given by the standard multinomial expression, i.e. the product of each trait frequency (p and $1 - p$, given that there are only two traits) raised to the powers k_1 and k_2 respectively.

$P(adopt\ 1)$ gives the probability of that row's demonstrator trait combination resulting in the observer adopting trait 1, incorporating the conformity parameter a. This is X_i in equation S2. In the first row/combination, $k_1 = 3 = n$, so $X_i = k_1/n = 1$. For the next three demonstrator combinations,

$k_1 = 2 = k_{max}$, so $X_i = k_i/n + a(n - k_i)/n$. And so on for the other demonstrator combinations. The final column contains the product of the coefficient, $P(forming)$ and $P(adopt\ 1)$. The sum of this final column gives the frequency of trait 1 in the next generation, p'_1:

$$p'_i = p^3 + 3p^2(1-p)(2/3 + a/3) + 3p(1-p)^2(1/3 - a/3) \qquad (S3)$$

which reduces to equation S1 because $s = 2$ and $n = 3$, as in Boyd and Richerson's (14) original formulation. When $s > 2$ or $n > 3$ the resulting recursion will not reduce to equation S1, but is derived in the same way from equation S2. In the case of $s = 2$, then the updated frequency of the other trait will equal $1 - p'$; when $s > 2$ then $s - 1$ traits need to be calculated using Equation S2.

Table S2: Example frequency table for calculating the frequency p_1' of trait 1 following conformity given two traits, 1 and 2 ($s = 2$) and three demonstrators ($n = 3$) See text for details. Dem=demonstrator, Coef=Coefficient, P(forming)=probability of that demonstrator combination forming randomly, P(adopt 1)=probability of adopting trait 1

Dem 1	Dem 2	Dem 3	k_1	k_2	Coef	$P(forming)$	$P(adopt\ 1) = X_1$	$Coef * P(forming) * P(adopt\ 1)$
1	1	1	3	0	1	p^3	1	p^3
1	1	2						
1	2	1	2	1	3	$p^2(1-p)$	$2/3 + a/3$	$3p^2(1-p)(2/3 + a/3)$
2	1	1						
1	2	2						
2	1	2	1	2	3	$p(1-p)^2$	$1/3 - a/3$	$3p(1-p)^2(1/3 - a/3)$
2	2	1						
2	2	2	0	3	1	$(1-p)^3$	0	0

Note that some combinations of $n > 3$ demonstrators will have more than one maximum k, e.g. for the trait combination {1,1,2,2,3} then $k_1 = 2$, $k_2 = 2$ and $k_3 = 1$, so k_1 and k_2 are both k_{max}. In such cases I assume no conformist effect and that adoption is unbiased. One could implement a more complex rule increasing the probability of adoption of the two or more joint-most-common traits, but for simplicity I leave such cases as unbiased.

Figure S2 shows the effect of increasing the number of demonstrators ($n > 3$) and adding more than two traits ($s > 2$) to the change in trait frequencies over time, with no assortation ($r = 0$). Increasing n increases the speed with which majority traits go to fixation. Increasing s causes the initially most-common trait to go to fixation, and all other traits to be eliminated.

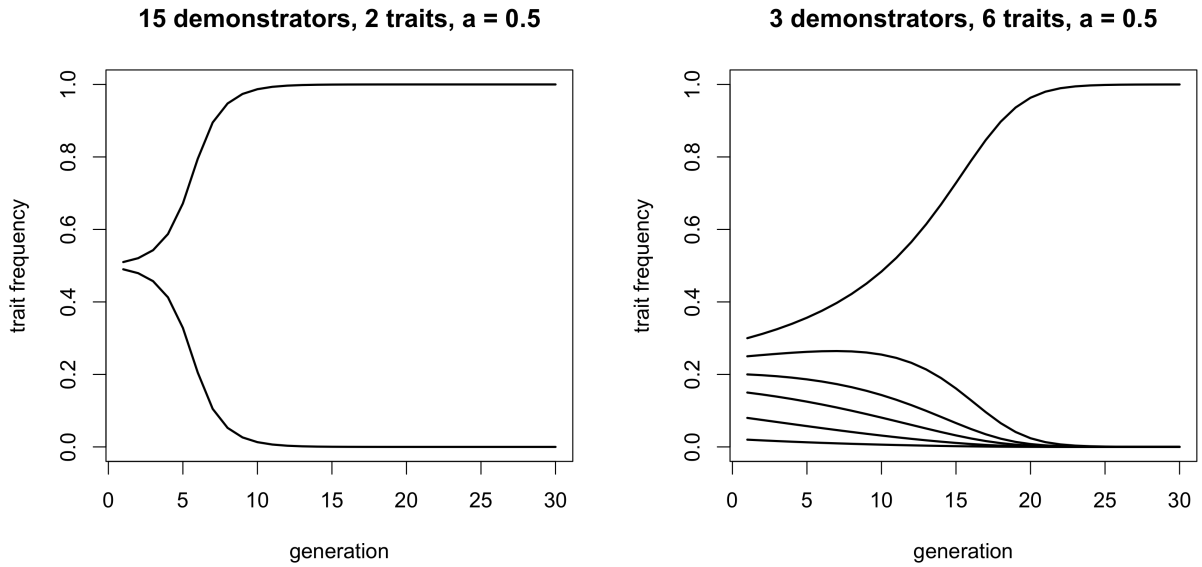

Figure S2: The effect of conformity on trait frequencies, for more than three demonstrators (left) and more than two traits (right). Increasing the number of demonstrators increases the strength of conformity (compare with Figure S1, left panel). For more than two traits, whichever trait is initially most frequent goes to fixation, even if this frequency is initially less than 0.5 (here initial trait frequencies were 0.3, 0.25, 0.2, 0.15, 0.08, and 0.02). Other parameters: r=0

Figure S3 shows the probability of adopting a trait given different frequencies of that trait in the population, which have become defining images of conformity in the cultural evolution literature. I show only the case of $s = 2$ for ease of interpretation. The left panel shows that a non-zero conformity parameter a generates S-curves, such that when the trait is common (its frequency is greater than 0.5) then the probability of adoption is exaggerated, and when the trait is uncommon (less than 0.5) then the probability of adoption is decreased, relative to the dotted line which shows unbiased, non-conformist transmission. Larger values of a generate stronger conformity curves. The right panel shows that increasing n also increases the strength of conformity, keeping a constant.

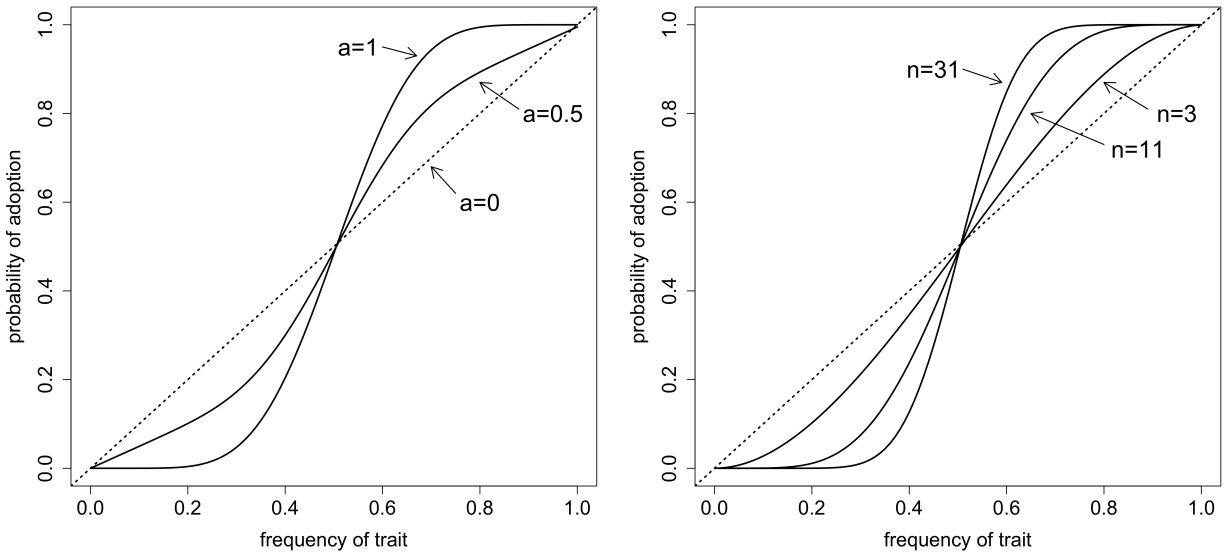

Figure S3: How conformity affects trait adoption. The y-axis shows the probability of adopting a trait as a function of that trait's frequency in the population. Here we assume only two traits (s=2). The dotted line shows unbiased, non-conformist transmission: the probability of adoption is exactly equal to the frequency in the population. The left panel shows different values of a for constant n (n=15). The right panel shows different values of n for constant a (a=1). Other parameters: r=0.

We now add non-random formation of demonstrators, or assortation. Boyd and Richerson (14) also implemented assortation, but they restricted its effect to a correlation r between two of three demonstrators. Here I wish to add a general assortation effect across all of n demonstrators, where $n \geq 3$. The simplest case would be where a fraction $1-r$ of demonstrator combinations form randomly as specified in Equation S2, and a fraction r form culturally homogenous sets of demonstrators who all possess the same cultural trait. In Table S2, this would be the first row (all demonstrators have trait 1) and last row (all demonstrators have trait 2). If we are interested in how p_i changes, then only one of these combinations will result in a change in p_i (the one where $k_i = n$) due to the X_i term. Assuming learners must possess the same trait p_i as the homogenous set of demonstrators, then a fraction p_i of individuals will learn from homogenous sets. Homogeneous sets always produce the same trait (again due to the X_i term), and so result in the same frequency of p_i as before transmission. In Equation S4, this is reflected in the rp_i term:

$$p_i' = (1-r)\Bigg[\sum_{k_1,k_2,...k_s=n} \binom{n}{k_1, k_2, ...k_s} \prod_{j=1}^{s} (p_j^{k_j}) \cdot X_i\Bigg] + rp_i \qquad (S4)$$

It is clear from Equation S4 that as r increases, the effect of conformity via X_i becomes weaker.

4 Individual-based version of Model 1

4.1 Description

In order to verify the recursion-based models that track trait frequencies, I created analogous individual-based models in which individuals and their traits are explicitly simulated. These individual-based models have the same assumption of s sub-populations and s traits. Now, however, we specify the number of individuals in each sub-population, N. This is different to n, which is the number of demonstrators sampled during conformist acculturation. n is also implemented in the individual-based models, so individuals pick n demonstrators from the N members of their sub-population. The individual-based simulations start with the same complete between-group structure as the recursion models, i.e. all N individuals in sub-population 1 have trait 1, all N individuals in sub-population 2 have trait 2, etc. F_{ST} is calculated in the same way as for the recursion-based model after calculating overall trait frequencies from individuals' traits. Migration occurs in the same way as the island model. Every time-step, each individual moves to a common migrant pool with probability m, and then randomly disperses across the newly vacant spots ignoring sub-population structure. Conformist acculturation is implemented slightly differently. Following all migration, each individual chooses n demonstrators from within their sub-population, and with probability a adopts the most common trait among those n demonstrators. Otherwise they retain their existing trait. This is conceptually the same as the recursion-based conformity described above in Section 3, but avoids the multinomial theorem implementation. For each of the n chosen demonstrators, with probability $1 - r$ that demonstrator is chosen randomly from the focal individual's sub-population. With probability r that demonstrator has the same trait as the focal individual. Consequently, when assortation parameter $r = 1$, then individuals only ever learn from demonstrators with the same trait as themselves. Parameter definitions for the individual-based model are given in Table S3. Full code of all models is available in https://github.com/amesoudi/migrationmodels.

Table S3: Parameter definitions for Model 1 individual-based simulations

Parameter	Definition
s	The number of sub-populations, and also the number of alternative cultural trait values
m	Migration rate: the probability in one time-step that an individual moves to a randomly chosen sub-population (equivalently, the proportion of the population that moves in one time-step)
n	The number of demonstrators from whom individuals learn during acculturation
a	Acculturation rate: the probability that an individual adopts the most-common trait among n demonstrators chosen from their sub-population, as opposed to retaining their existing trait. When $a = 1$, there is 100% chance of copying the most-common trait (if there is one).
N	The number of individuals in each sub-population (giving Ns individuals in the entire population)
r	The probability that a demonstrator is chosen who has the same trait as the focal individual, rather than chosen at random.

4.2 Results

Figures S4, S5 and S6 show the individual-based model results equivalent to the recursion-based model results shown in Figures 1, 2 and 3. There is very little difference between the two models, despite their different implementation, increasing our confidence in the robustness of the conclusions. There is a slight tendency for F_{ST} to be lower in the individual-based model than the recursion-based model. This may be due to drift which operates only in the finite populations of the individual-based models. If a trait is lost due to drift, then diversity will be reduced. Figure S7 repeats Figure 2/S5 but with larger n than is computationally feasible with the recursion-based model. Here we can see that increasing n above 13 does not change the dynamics, except at very low values of a when migration is very high (Figure S7C).

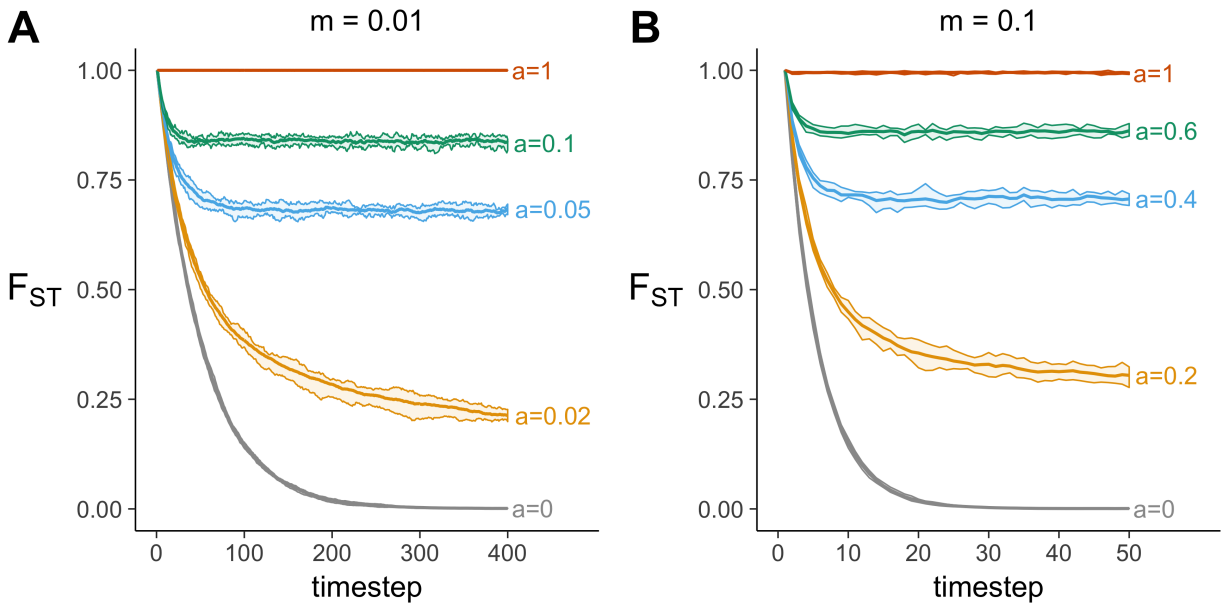

Figure S4: Time series showing changes in F_{ST} over time for (A) a low migration rate m=0.01 and (B) a high migration rate m=0.1, at varying strengths of acculturation, a, in the individual-based model. Other parameters: s=5, n=5, N=1000; results are the average of 10 independent simulation runs.

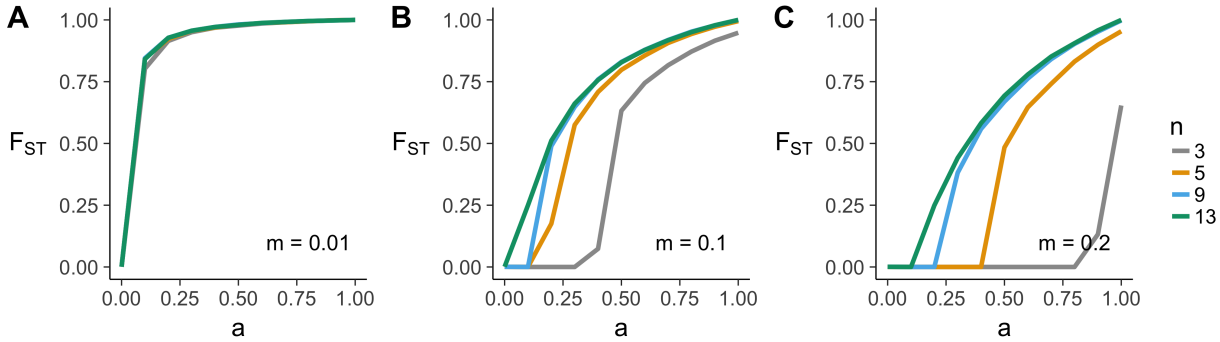

Figure S5: The relationship between a and F_{ST} at three different migration rates, and different values of n, for the individual-based model. Other parameters: s=5, 500 timesteps, N=1000; results are the average of 10 independent simulation runs.

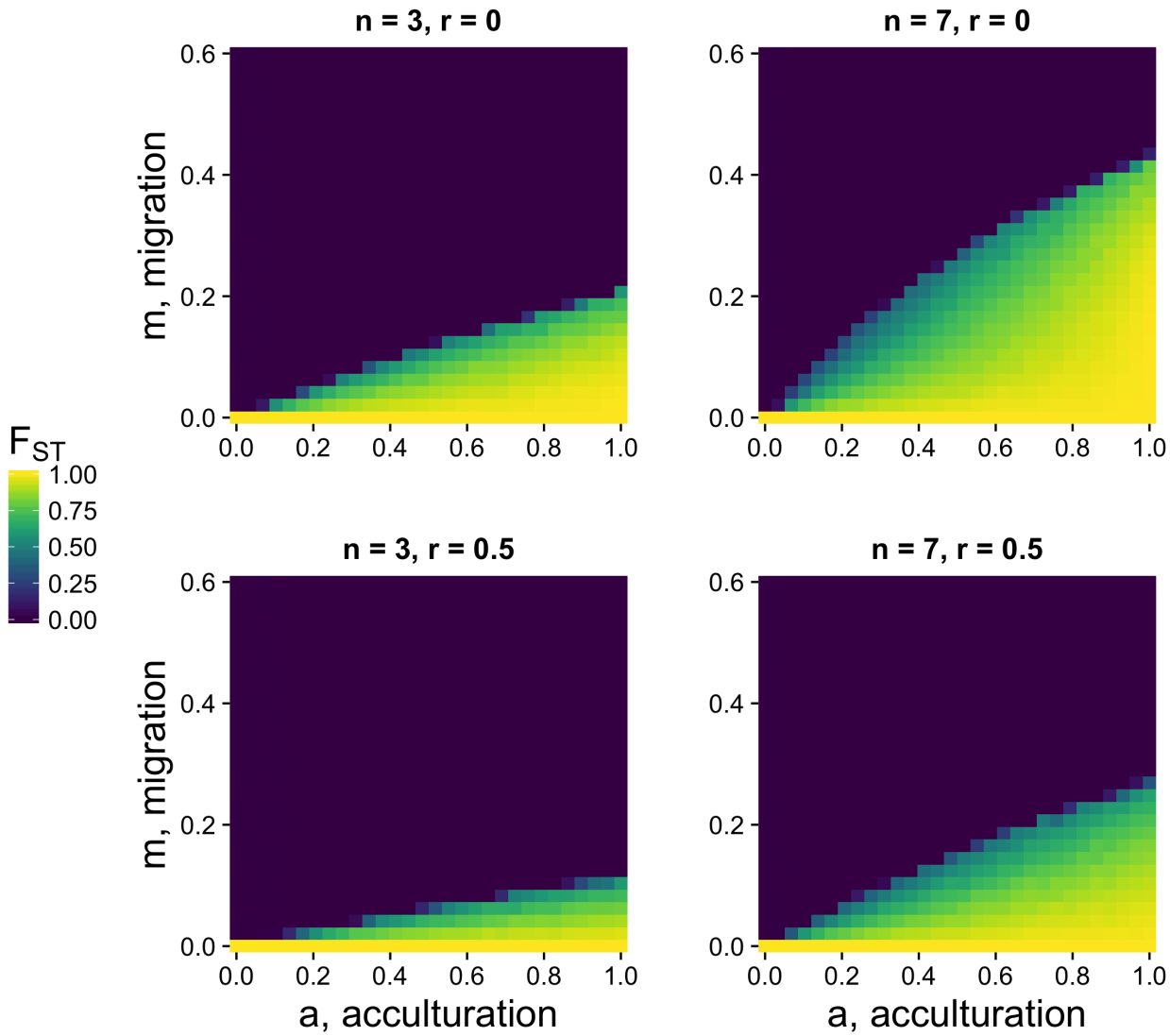

Figure S6: Heatmap showing F_{ST} for varying acculturation rates, a, and migration rates, m, separately for three different values of n, the number of demonstrators, for the individual-based model. Other parameters: s=5, N=1000, 500 timesteps; results are the average of 10 independent simulation runs.

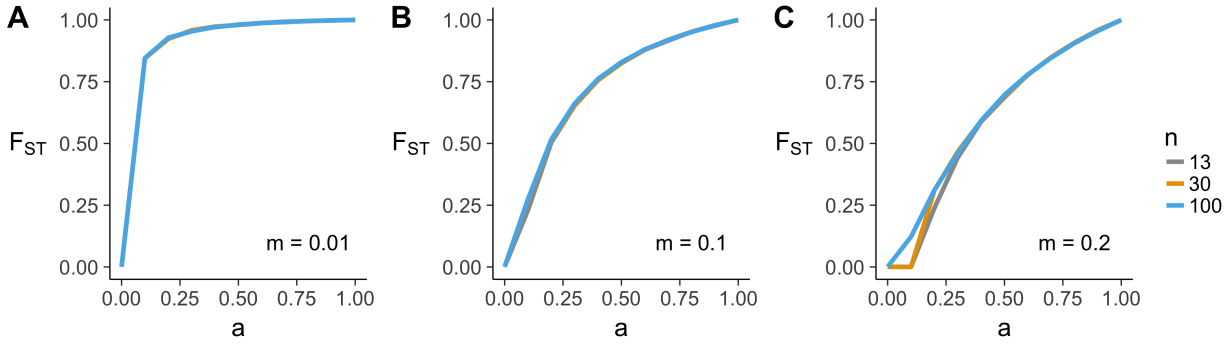

Figure S7: The relationship between a and F_{ST} at three different migration rates, for three large values of n, for the individual-based model. Other parameters: s=5, 500 timesteps, N=1000; results are the average of 10 independent simulation runs.

5 Model 2 fitness plots and assumptions

The fitness functions given in the main text are a specific cooperation version of the general fitness functions for coordination games provided in Boyd & Richerson (17). Figure S8 plots the fitness of cooperators (w_c, blue line) and defectors (w_d, red line) at different frequencies of cooperators, p, equivalent to Figure 1 in (17). The lines cross at p^*, as given by Equation 4 in the main text. This point p^*, where the fitness of cooperators and defectors is equal, is an unstable equilibrium for payoff-biased within-group social learning (as determined by L). To ensure that fitnesses are always positive, I assume that $b > c$, $b > v$ and $c + u < 1$.

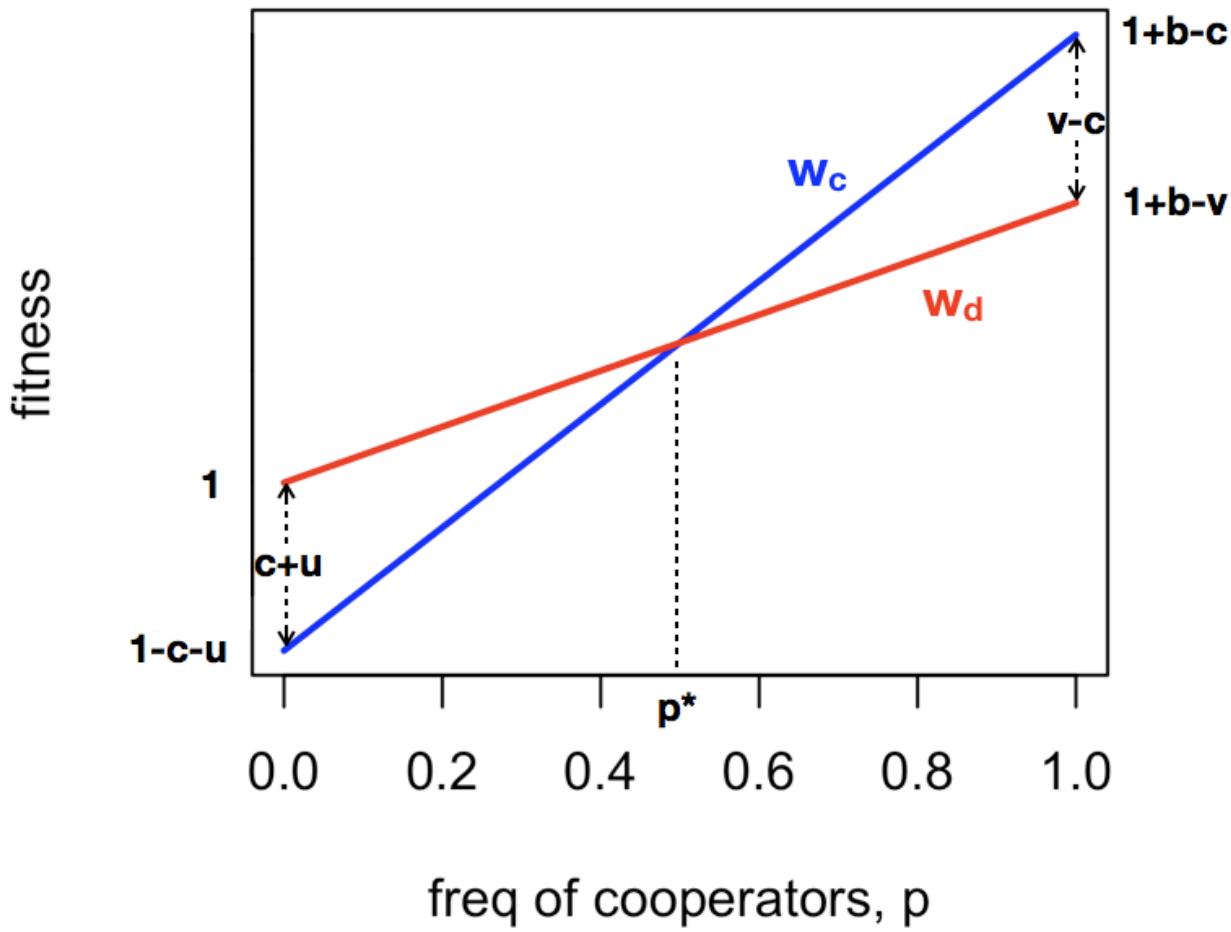

Figure S8: Fitnesses of cooperators (w_c, blue line) and defectors (w_d, red line) at different frequencies of cooperators, p. Annotations show how fitness parameters affect these functions, and p^* indicates where the lines cross.

The fitness parameter values were chosen in Figure S8 so that $p^* = 0.5$ and the basin of attraction within which cooperators have higher fitness than defectors ($w_c > w_d$ or $p > p^*$) and the basin of attraction within which defectors have higher fitness than cooperators ($w_d > w_c$ or $p < p^*$) are equal. Other fitness parameter values give different values of p^* and alter the relative sizes of these basins of attraction. The easiest way of doing this is varying v, the punishment cost borne by defectors. Figure

S9 shows fitness plots for three different values of v, in the centre with equal basins of attraction (as in Figure S8), on the right where cooperators have a larger basin of attraction, and on the left where defectors have a larger basin of attraction. This has consequences for the action of payoff-biased within-group social learning (L) by changing the unstable equilibrium point.

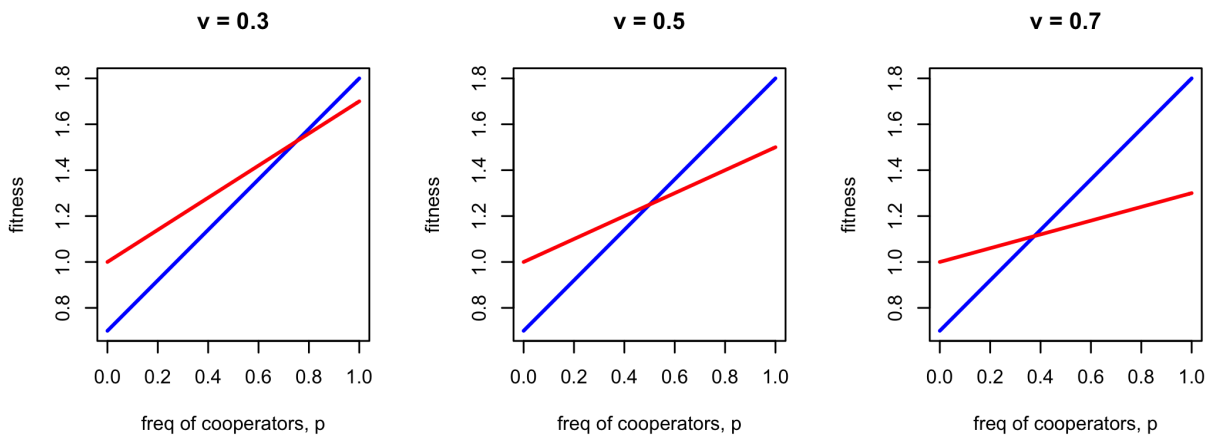

Figure S9: Fitnesses plots for three different values of v, which determines the cost of being punished for defectors. When v is large, cooperators have a larger basin of attraction. When v is small, defectors have a larger basin of attraction. Other parameters: b=1, c=0.2, u=0.1.

Equation S5 gives the mean population fitness W. Figure S10 plots this quadratic function of p.

$$W = pw_c + (1-p)w_d = (u+v)p^2 + (b-v-c-u)p \qquad (S5)$$

To keep the model simple I assume that W is always greater than 1, in other words, a population entirely composed of defectors ($p = 0$) always has lower fitness than any population containing any cooperators ($p > 0$). In terms of Figure S10, this would mean that the green W line never drops below $W = 1$. To ensure this, I assume that $(b-c) > (u+v)$. Finally, the parameter μ in Equation 5 ensures that the weighted migration rate $m(W-1)$ never exceeds the baseline migration rate m. This is done by setting μ to be the reciprocal of the maximum value of $W-1$ which occurs at $p = 1$, so $\mu = 1/(b-c)$. Similarly, γ in Equation 6 ensures that the change in p due to payoff-biased social learning always scales from 0 to L. From Figure S8, the maximum absolute fitness difference between cooperators and defectors ($w_c - w_d$) is either $v - c$ or $c + u$, whichever is larger, so $\gamma = 1/[max(v-c, c+u)]$.

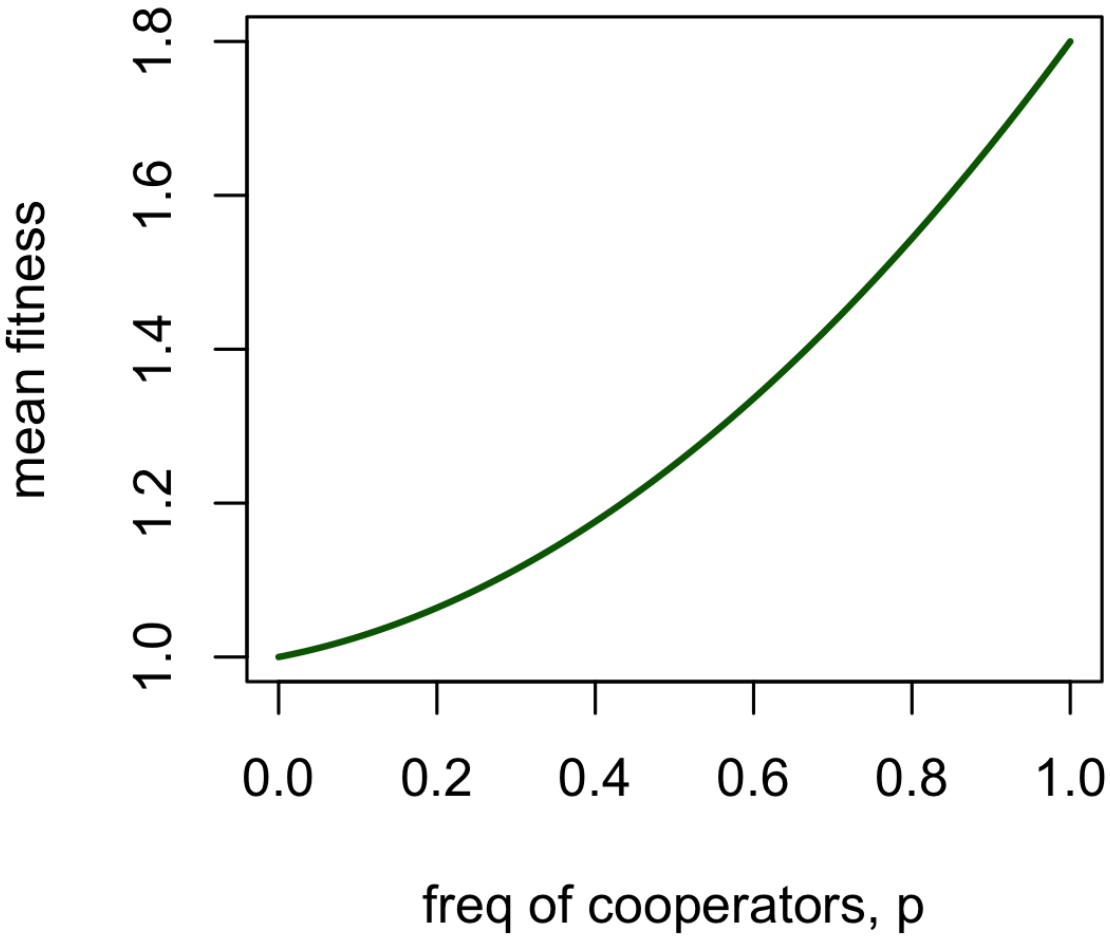

Figure S10: Mean sub-population fitness W as a function of p, as given by Equation S6. Parameters: b=1, c=0.2, u=0.1, v=0.5.

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