



# An investigation of the relationship between innovation and cultural diversity

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## ABSTRACT

In this paper we apply reaction–diffusion models to explore the relationship between the rate of behavioural innovation and the level of cultural diversity. We investigate how both independent invention and the modification and refinement of established innovations impact on cultural dynamics and diversity. Further, we analyse these relationships in the presence of biases in cultural learning and find that the introduction of new variants typically increases cultural diversity substantially in the short term, but may decrease long-term diversity. Independent invention generally supports higher levels of cultural diversity than refinement. Repeated patterns of innovation through refinement generate characteristic oscillating trends in diversity, with increasing trends towards greater average diversity observed for medium but not low innovation rates. Conformity weakens the relationship between innovation and diversity. The level of cultural diversity, and pattern of temporal dynamics, potentially provide clues as to the underlying process, which can be used to interpret empirical data.

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## 1. Introduction

Recent decades have witnessed considerable interest in the mathematical modelling of the dynamics of cultural change. A number of researchers have adapted the methods of theoretical population genetics to study the dynamics of cultural change through time, as well as the co-evolution of genes and culture (Boyd and Richerson, 1985; Cavalli-Sforza and Feldman, 1981; Feldman and Cavalli-Sforza, 1976; Feldman and Laland, 1996; Henrich and McElreath, 2003; Richerson and Boyd, 2005; Enquist et al., 2007). Such models include analysis of a variety of other forms of cultural transmission (Boyd and Richerson, 1985; Cavalli-Sforza and Feldman, 1981; Feldman and Cavalli-Sforza, 1976), application of neutral genetic drift models to study the evolution of cultural traits (Bentley et al., 2004), and of phylogenetic methods to reconstruct the history of diverse cultural traits (Gray and Jordan, 2000; Holden, 2002; Holden and Mace, 2003; O'Brien and Lyman, 2003).

While the mathematical modelling of culture is a rapidly developing and highly productive discipline, one topic that has received comparatively little attention is the relationship between innovation and cultural diversity. Nor has this topic been addressed by the diffusion research tradition (Rogers, 2003), which explores how, why, and at what rate new ideas and technology spread through cultures. This is paradoxical for two reasons: first, at least since Boas, widely regarded as the father of American anthropology

(e.g. Boas (1911)), understanding why people are different (i.e. the causes of cultural diversity) has been recognized as one of the major objectives of the social sciences. Second, it would be difficult to find another topic in anthropology and archaeology that has played as important a role as innovation in framing arguments about why and how human behaviour changes (O'Brien, in press). Nineteenth century ethnologists, such as Tylor (1871) and Morgan (1877), viewed the production of novelties as the evolutionary driver that propels cultures up a hierarchy of cultural complexity. Innovation was equally important in the work of later cultural evolutionists such as Steward (1955) and White (1959), who regarded it as a key component that a group needs to meet the challenges of its physical and social environment. American culture historians of the twentieth century routinely looked to diffusion and trade as a source of innovations, and hence of cultural change and diversity (e.g. Ford, 1969). Even contemporary debates over the legitimacy of cultural phylogenetics (e.g. Borgerhoff Mulder et al. (2006)) hang in part on the extent to which cultural diversity can be explained by divergent tradition, independent invention, or the diffusion of innovation. This issue is also central to attempts to comprehend the processes underlying the human capacity for cumulative culture (Ghirlanda and Enquist, 2007). Accordingly, understanding of the relationship between innovation and diversity would engender widespread interest.

To date, empirical analysis of this question using the archaeological or historical record has been hindered by the difficulty that often only one or two different time periods are considered in a given study, or the fact that the study is focused on the comparison of the temporal evolution of two variants (e.g. the replacement

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of horses by tractors in agriculture, (Mattingly, 1987)). Here we develop a mathematical analysis of the relationship between innovation and diversity, hoping that this will provide a theoretical framework that will encourage further empirical study. Indeed, our analyses not only shed light on the processes of innovation and cultural change, but also provide methods by which the mechanisms of innovation can be inferred from the degree of diversity.<sup>1</sup>

Our study is designed to address the following issues. First, while it may be intuitive to assume that innovation will generate cultural diversity in the short term, it is far from clear that innovation will lead to enhanced cultural diversity in the longer term, or at equilibrium. In principle, technological innovations could merely displace established technology, without increasing long-term diversity. Accordingly, we ask under what circumstances innovation promotes cultural diversity. Second, we explore whether there is a threshold rate of innovation that is necessary to support the accumulation of cultural diversity. Third, while many innovations can be characterized as refinement or modification of an established variant (Basalla, 1988), other cases might be perceived as entirely independent invention. The latter category include serendipitous or accidental discoveries, for which X-rays, electromagnetism, ozone, photography, dynamite, the gramophone, vaccination, radioactivity, classical conditioning, and penicillin are all examples (Simonton, 1995). We investigate whether these two alternative forms of innovation may impact differentially on cultural diversity. Fourth, in the light of this analysis, we consider whether it might be possible to draw inferences about the innovation mechanism (independent invention versus refinement) on the basis of the observed level of cultural diversity. Fifth, we explore how the relationship between innovation and diversity will be affected by biases in cultural transmission. Some forms of social learning (most obviously, conformist transmission, where individuals preferentially adopt the majority trait) may counteract any positive effect of innovation on cultural diversity.

We apply reaction–diffusion models to investigate how both independent invention and the modification and refinement of established innovations affect cultural diversity, building on earlier studies of language competition (e.g. Kandler and Steele (2008) and Pinasco and Romanelli (2006)), cultural hitchhiking (Ackland et al., 2007), and prestige bias (Ihara, 2008), that exploit similar methods. The models comprise reaction, diffusion and competition components, which collectively are well-suited to capture aspects of the spread of an innovation in a finite population. Using established population ecology metrics, we propose a number of distinct measures of cultural diversity (see Appendix B), illustrating how each is affected by the innovation rate. We begin by assuming that social learning is unbiased (acquired in proportion to the frequency of the variants in the population), but go on to investigate the impact of both frequency-independent and frequency-dependent cultural transmission biases.

## 2. The model

A detailed mathematical description of the model can be found in Appendix A; here we present an accessible summary. We develop and analyse a model that describes the spread dynamics of  $n$  competing (mutually exclusive) variants of a specific cultural trait within a population. Such variants might represent alternative beneficial subsistence techniques, technologies, religious beliefs,

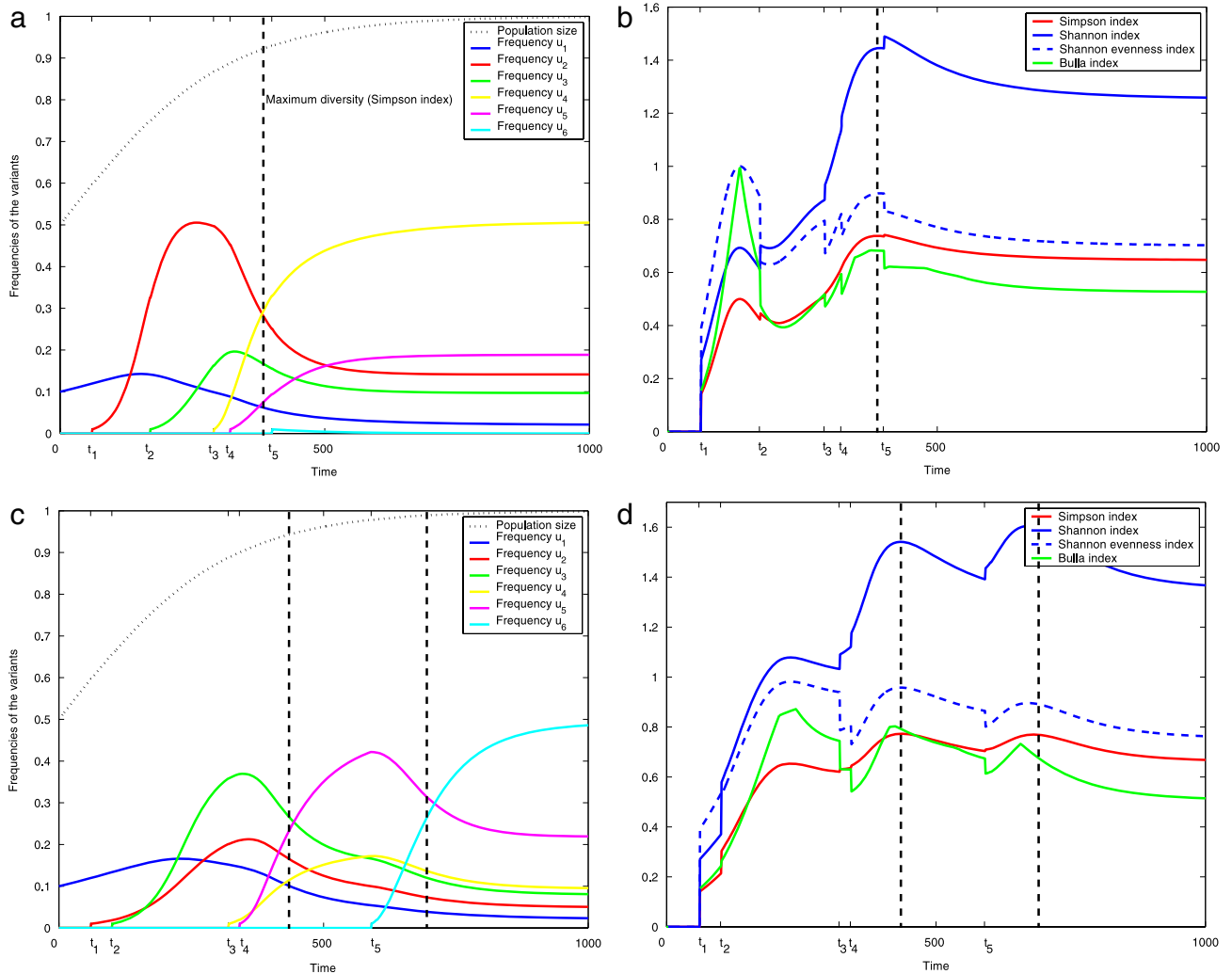
or languages. Obviously cumulative increases in “diversity” may occur in cases where innovations do not compete, and our conclusions regarding the relationship between innovation and diversity are restricted to competing cultural variants. Using a continuous differential equation based approach, we determine the temporal and spatial changes in the frequencies of  $n$  variants, denoted by  $u_1, u_2, \dots, u_n$ . Individuals can adopt only one variant at a time. (We have found that analysis of situations where individuals are allowed to adopt more than one variant at the same time leads to similar results.) We assume a constant and homogeneous environment, which we model through temporally and spatially constant model parameters. Although the model possesses a deterministic nature and therefore ignores drastic and rare events, its results can be regarded as null hypotheses. Failures in the predictions of the model can be understood as evidences of the significant impact of rare changes on the competition dynamic (Ackland et al., 2007).<sup>2</sup>

Variant frequency change is determined by two main components—diffusion and growth. The diffusion component models the spread of an innovation from a specific location in space as a random walk, with density-dependent mixing, equivalent to the random spread of an innovation through direct contact between individuals. The propensities of variants to spread out in space vary and are described by the ‘diffusion coefficients’ (denoted by  $d_i$ ). The reaction term describes the increase in frequency of each variant amongst naive individuals (individuals that have not yet adopted the trait), according to a specific ‘growth’ parameter, where a conventional logistic growth is assumed, as well as representing the effects of competition. Initially we assume that unbiased social learning (or asocial adoption) underpins the adoption process, but later we consider various kinds of cultural transmission bias. Variants differ in their growth propensities, denoted by  $a_i$ , depending on the benefits each conveys to its adopters. In addition, growth is influenced by individuals that have already adopted a variant switching to an alternative variant. Variants hinder each other in growth, with the degree of hindrance determined by variant frequencies and ‘switch coefficients’, denoted  $c_{ij}$ , specifying the proportion of adopters of variant  $i$  that switch to adopt variant  $j$ . The more beneficial a variant, the less likely are its adopters to switch and at the same time the more likely it is the preferred target of switching, which restricts the growth of competing variants. Variants need not be present at the beginning ( $t = 0$ ) of the analysis, and can be invented at later time points  $t_k$ . The time between two inventions is modelled by an exponential distributed variable  $\tau \sim \exp(\lambda)$ , with innovation rate  $\lambda$ .

We consider two classes of innovation, *modification of an existing variant* and *independent invention*, and represent these in the model through choice of appropriate values of the intrinsic growth rate  $a_i$  and competition coefficient  $c_{ij}$  parameters. While we assume that modification can result in both an improvement and a worsening of the existing variant, here we focus on improvement. Improvement implies that the newly invented variant offers adopters benefits over the original, in which case we assume it will be preferred to the original, and that individuals who have already adopted other variants will be more likely switch to the improved variant than the original. These expectations can be implemented by (1) assuming a higher intrinsic growth coefficient for the improved variant over the original, and (2) imposing the constraints  $c_{i0} < c_{0i}$  and  $c_{k0} < c_{ki}$ , where  $c_{i0}$  indicates how much the original variant hinders the improved variant in growth,  $c_{0i}$  describes the reverse relation,  $c_{ki}$  describes the competition between the improved variant and the other

<sup>1</sup> Currently there is no well established method for measuring cultural trait diversity, nor even a well characterized notion of a cultural trait. It is apparent that the specific definitions and methods deployed may influence the absolute level of diversity observed. We nonetheless assume the existence of a framework regarding how the cultural variants are defined and measured, and do not expect such definitional factors to affect our qualitative conclusions.

<sup>2</sup> Obviously, such failings can also result from inadequate assumptions that fail to capture the underlying basic processes.



**Fig. 1.** (a) and (c) Representative frequency time course for six competing variants, with (b) and (d) showing the corresponding diversity measures. (a) and (b) represent modifications that may or may not be improvements (and also to some degree reflects the behaviour of independent inventions), while (c) and (d) represent the case where all newly invented variants are improvements on pre-existing variants. The first variant is invented at  $t = 0$  and variant  $k$  is invented at random time points  $t_k = \sum_{i=1}^k \tau_i$  with  $\tau_i \sim \exp(0.01)$ . The innovation rate  $\lambda = 0.01$  leads on average to six innovations during the period  $[0, 600]$ .

present variants, and  $c_{KO}$  the competition between the original variant and the remaining variants.<sup>3</sup> As a result of the described procedure the invented variants can be ordered hierarchically in terms of the benefits they offer to their adopters. In the case of *independent invention*, we assume that a variant is invented without knowledge of established variants, and represent this through allotting parameter values that are randomly selected relative to the variants present in the population.

In our analyses, we consider both the stable equilibria, that is, the long-term ratios of the competing variants, and the temporal dynamics in the approach to equilibria. We show that the stable equilibria are coexistence states, here denoted by  $(u_1^*, u_2^*, \dots, u_n^*)$ . Coexistence means that all variants are present in the population, although, depending on the specific circumstances, they may have a negligibly small frequency, and in a stochastic system might plausibly be lost. Interestingly, due to the involved spatial

diffusion process the obtained equilibria are spatially uniform,<sup>4</sup> which means the variant's frequency distribution is constant over the entire space. Therefore we focus on the description of the competition dynamic over time, rather than space. However, the use of a spatially explicit model greatly enhances the biological and cultural plausibility of our analysis: independent inventions are not all devised in the same place, but rather are distributed and diffuse through space, while competition between variants depends on local (rather than global) variant frequencies.

Quantitative measures of cultural diversity were developed through borrowing related biodiversity, species richness and evenness measures from biology (see Appendix B). We draw on four established metrics: (i) the Simpson and (ii) Shannon indices, which incorporate variant richness and variant evenness in the evaluation of diversity, (iii) the Shannon evenness index, which considers variant evenness only, and (iv) a diversity measure introduced by Bulla (1994) that is designed to be sensitive to the presence of rare variants.

<sup>3</sup> Note that we assume that variants that offer benefits to the user are more likely to be retained than less effective variants. While we acknowledge the possibility that superficially attractive variants could be adopted, but then subsequently be found to be inadequate and rejected, here we prefer to concentrate on the more general case.

<sup>4</sup> Spatially dependent equilibria can be obtained by, for instance, assuming a heterogeneous environment where the level of benefit of the variants varies in space or the domain shows a certain non-convex pattern (e.g. a connected island domain).

### 3. Results

#### 3.1. Innovation and short-term dynamics

Fig. 1 illustrates the change in frequencies over time, and the corresponding impact on diversity, of six competing variants, where variants 2–6 are each a modification of an already existing variant.<sup>5</sup> In order to illustrate the long-term effects of innovation it is convenient to distinguish between two time periods—an *innovation period*  $[0, t_{inv}]$  during which innovation occurs and a *stabilization period*  $[t_{inv}, t_{stab}]$  where no innovation occurs and the stable long-term frequencies are reached. After stabilization, variant frequencies settle down to the stable coexistence state  $(u_1^*, u_2^*, \dots, u_6^*)$ , although it is apparent from Fig. 1 that some variants have a negligible small frequency at equilibrium. In (a) and (b), not all modifications are improvements. Here, variant 4 is the most beneficial variant and establishes itself at the highest frequency at equilibrium. However, the time course of variant 2's frequency illustrates that other variants can increase to equivalent frequencies in the short term. With unbiased social learning the exact times  $t_k$  and order of the innovations' inception have no influence on the stable equilibrium, although they do change the course of the competition dynamics.

Fig. 1b shows how the spread of the innovations affects cultural diversity, as measured by our four indices. Reassuringly, all indices produce the same general patterns over time, although their absolute values and micro-dynamics vary considerably. It is immediately apparent that, contrary to the widespread expectation that innovation will inevitably increase diversity, in the short term, cultural diversity does not always increase with innovation, and all diversity measures show marked decreases at some juncture. Indeed, some diversity indices (Shannon evenness index, Bulla index) typically decrease with innovation.

Prior to the invention of the second variant ( $t_1$ ) all diversity measures are zero, since only one variant is present, and at this juncture an immediate increase in all indices is observable. However, from invention points  $t_2, \dots, t_5$  the indices behave differently. The Shannon evenness index and the Bulla index evaluate only the evenness of the frequency distribution and so typically decrease at every invention point  $t_2, \dots, t_5$  since evenness usually decreases by introducing a new variant at low frequency. In contrast, the other indices show an increase in diversity at invention points, because they incorporate the number of variants, as well as evenness. The indices reach their maxima when variant 2 and variant 4, the most advantageous variants in the sample, have similar frequencies, a pattern that appears general, since this constellation represents the most even state of the frequency distribution. However, from this point all diversity measures decrease, as the dominant variant gradually displaces its competitors. The presence of a dominant variant, by which we mean an innovation that conveys a significantly higher benefit to adopters than other variants, almost always reduces cultural diversity in the longer term.

In the short term, the temporal dynamics for independent invention resembles that for randomly generated modification (Fig. 1a and b). Indeed, since Fig. 1a depicts a situation in which newly invented variants can be both superior and inferior to existing variants, the principal difference between this kind of innovation through modification and independent invention is

merely the magnitude of the differences in parameter values between variants. It is only when innovation through modification repeatedly generates improvements that we witness qualitative differences in the patterns of diversity generated by the two types of innovation.

Fig. 1c and d illustrate the situation where all newly invented variants are improvements on pre-existing variants. Here the dynamics exhibit predictable patterns that are highly dependent on the innovation rate. The impact of innovation on long-term diversity is variable across indices, with those measures solely dependent on evenness less affected by new variants in the longer term than other measures. We have established that provided there is sufficient average time between innovations for the most beneficial variants to reach high frequency, a cycling pattern of diversity will emerge. The local maxima of the diversity indices are reached when the two most beneficial variants have similar frequencies (dashed lines).

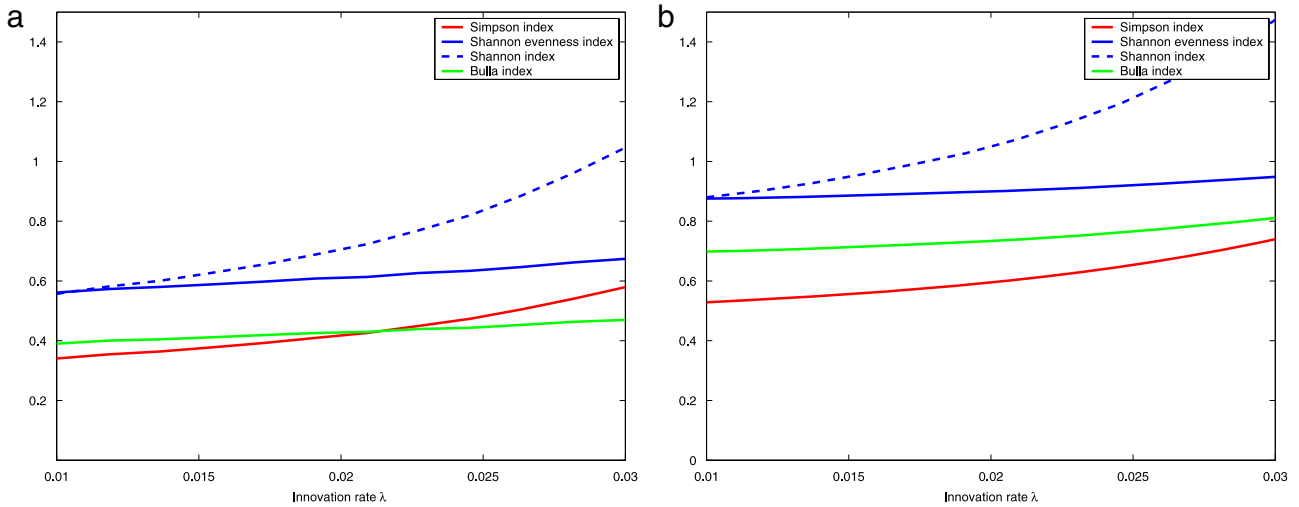
Fig. 1d illustrates two primary processes that underpin the relationship between innovation and diversity. Discounting evenness measures, the introduction of new variants typically increases diversity substantially in the short term, as the new fit variant increases in frequency; however, once the most beneficial variant becomes dominant, the periods following inventions typically witness reductions in diversity, as the fittest variant out-competes the alternatives. If the time between innovations is comparatively short (a high innovation rate), the dynamics are dominated by the first of these processes, and diversity increases steadily over time. At the other extreme, long periods between innovations (low innovation rate) allow the second process to dominate, and we witness regular cycles in diversity, but with no increase, or only modest increases, in long-term diversity. Between these extremes we witness cycling in diversity associated with a saw-tooth-like increase in diversity with each innovation. We propose that the detection of these characteristic patterns of diversity change in the historical or archaeological record may potentially allow researchers to draw inferences about both the rate of innovation and the extent to which innovations are refinements.

#### 3.2. Innovation and long-term dynamics

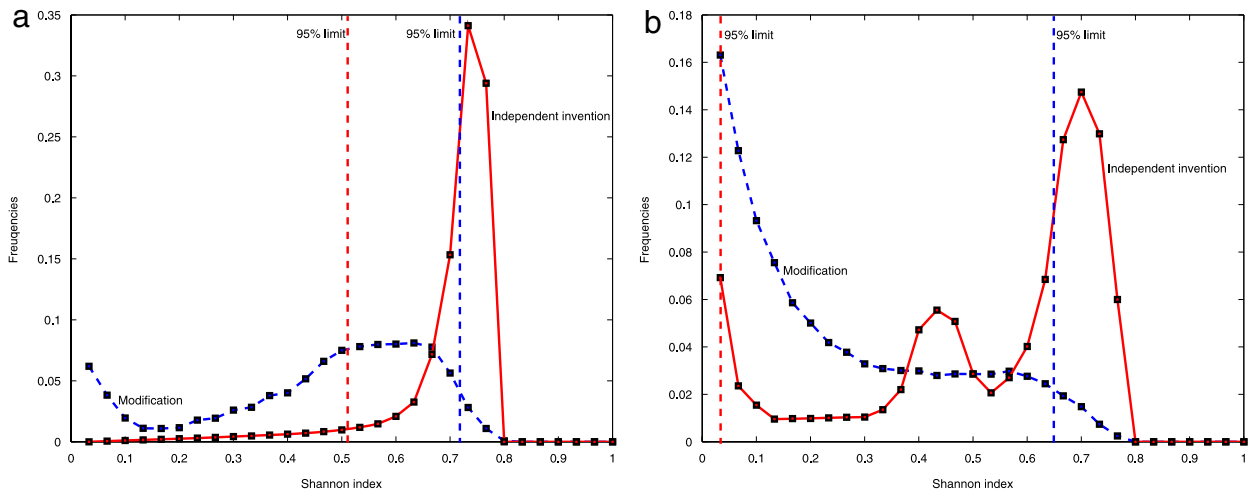
We now consider the relationship between innovation rate and cultural diversity at equilibrium. We assumed that the time between two innovations is determined by an exponential distributed variable  $\tau \sim \exp(\lambda)$ , where the innovation rate  $\lambda$  models how frequent innovations occur. In our model set-up it means that on average  $t_{inv}/\lambda$  variants are invented during the period  $[0, t_{inv}]$ . Fig. 2a shows the relation between the average level of cultural diversity and innovation rate  $\lambda$  where there is improvement of an existing variant, and Fig. 2b where there is independent invention. The average level is obtained by 10,000 simulations<sup>6</sup> for every value of  $\lambda$ . In both cases we obtain an almost linear relationship: the higher the rate of innovation the higher the cultural diversity. This result confirms the intuitive expectation that an increase in the number of variants is associated with an increase in cultural diversity, although the absolute magnitude of the increase in diversity with innovation rate is frequently

<sup>5</sup> As stated before, our model leads to spatially constant equilibria. Therefore the following figures illustrate the time course of the competition dynamic at a fixed spatial point and for the sake of simplification we call the times  $t_k$  invention times of the  $k$ th variant whereas in the spatially explicit formulation of the model they are the arrival times of variant  $k$  at location  $x$ .

<sup>6</sup> The simulations are carried out as follows. In the case of modification, the rank of every newly invented variant in the already existing order of variants is chosen randomly (that means whether the new variant is an improvement or worsening compared to every already existing variant is assigned at random), while the growth and competition coefficients are determined accordingly to the above procedure. In contrast, in the case of independent invention the growth and competition coefficients are modelled by uniform distributed variables. However, importantly, the possible parameter ranges in both cases are the same.



**Fig. 2.** Relation between the average level of cultural diversity and innovation rate  $\lambda$  for (a) innovations through improvement, and (b) independent invention. For each of 40 values of  $\lambda$  from 0.01 to 0.03, a random number of invented variants were selected, with randomly chosen degrees of advantageousness. Repeating this procedure, and averaging over 10,000 runs, leads to an average level of cultural diversity for the chosen innovation rate. Similar results are obtained when the adoption rates  $a_i$  and competition terms  $c_{ij}$  are negatively correlated.



**Fig. 3.** Frequency distributions of the Shannon index for innovation through modification (dashed lines) and independent invention (solid lines), (a) without conformity, and (b) with strong conformity. We assume a situation where four variants are invented during a given time period. With strong conformity, independent invention favours situations where different numbers of variants have similar frequencies.

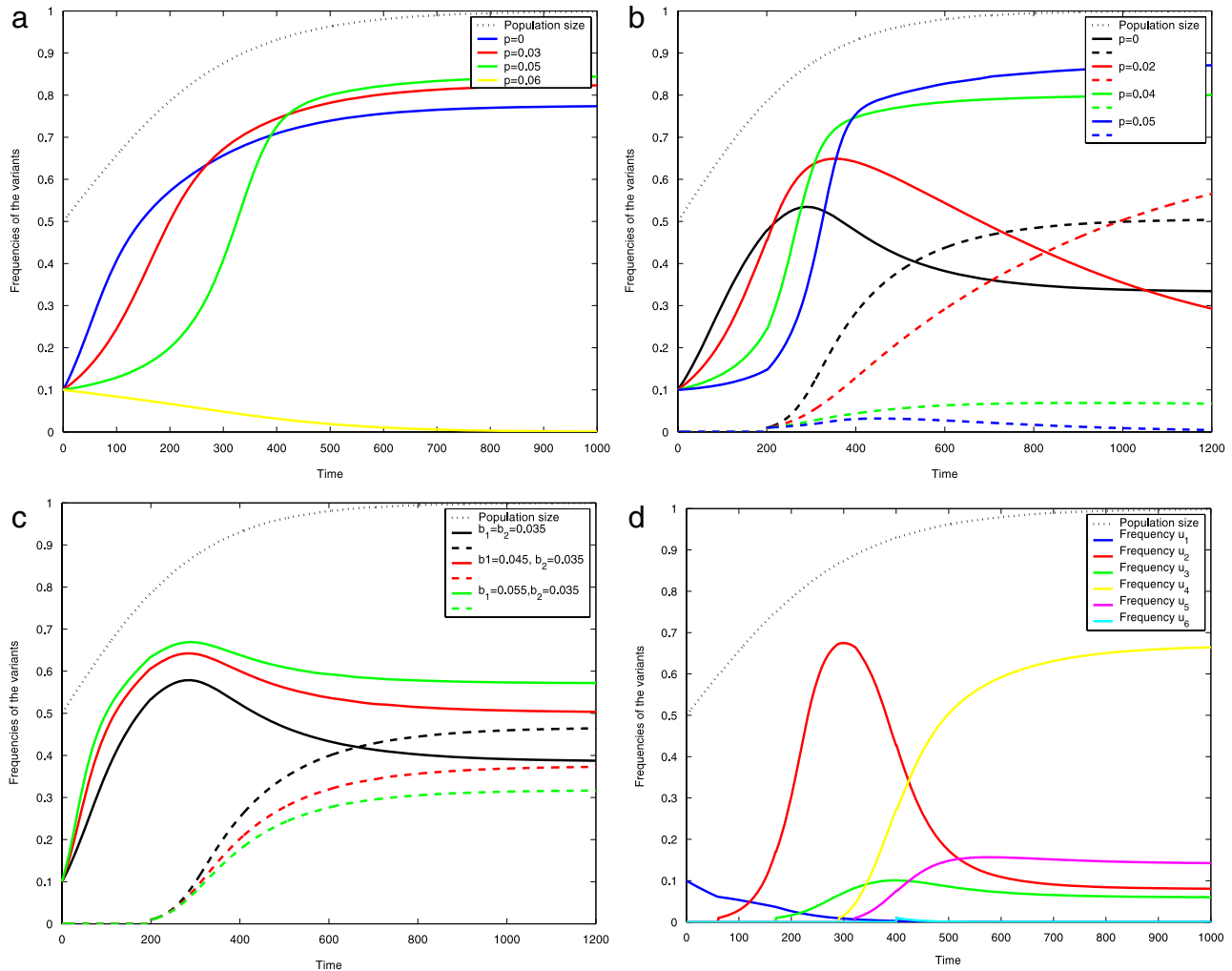
surprisingly modest. A doubling of the innovation rate can be associated with an increase in long-term cultural diversity of approximately 6%–32%. Increases on the lower end of the scale are obtained by evenness indices (Shannon evenness index, Bulla index), while increases on the higher end are obtained by the indices that also incorporate the number of variants present.

Independent invention typically generates greater diversity than modification. Over 10,000 runs we observe a maximum error margin of 4% (based on a 95% confidence level) for the four diversity measures, which means that the observed differences between the two types of innovation cannot be attributed to random effects of the Monte Carlo simulation method, and there is a genuine difference in the typical level of diversity associated with the two types of innovation. The higher diversity level associated with independent invention results from the fact that if individuals invent independently the chance of creating a variant that is strongly dominant over all others is lower compared with the situation of improvement, and as a result evenness and cultural diversity increase. Furthermore, we find that the slopes of the diversity measures are frequently steeper for modification than for independent invention. For modified variants we often observe

for cases with few variants (indicated by small  $\lambda$  values) that the most advantageous variant has a significant frequency advantage. In contrast, situations with more variants are typically more even because the chance of inventing two comparable beneficial variants is increased. This effect is most apparent in the Shannon evenness index; the more variants are invented the more even becomes the distribution. Conversely, because of the reduced likelihood of a dominant variant in situations of independent invention we do not obtain the same slope.

These findings raise the question of whether it might be possible to distinguish between the two different sources of innovation, modification and independent invention, on the basis of the observed level of cultural diversity. To explore this question we assume a situation where four variants are invented during a given time period. Our aim is to determine the probability of obtaining a particular level of cultural diversity under the assumptions of modification or independent invention.

Fig. 3a shows the frequency distributions of the Shannon index of the equilibria ( $u_1^*, u_2^*, u_3^*, u_4^*$ ) obtained by 10,000 simulations. We can see that the two sources of innovation result in different characteristic diversity distributions. While independent invention



**Fig. 4.** Influence of conformity (expressed by the parameter  $p$ ) on the spread dynamic of variants. (a) A single-variant system. (b) Two variants, where variant 1 is represented by the solid lines and variant 2 by the dashed lines. Here the variants are equally favoured by transmission biases but variant 2 has a competitive advantage to variant 1 ( $c_{12} > c_{21}$ ). (c) Influence of direct and indirect transmission biases (expressed by the parameter  $b$ ) on the spread dynamic of two variants (again, variant 1 is represented by the solid lines, and variant 2 by the dashed lines). Conformity in the population is at a moderate level but variant 2 has a benefit advantage compared with variant 1 ( $c_{12} > c_{21}$ ). The black lines illustrate the situation where both variants are supported in the same way by direct and indirect biases. Because of its benefit advantage variant 2 achieves a higher frequency than variant 1 at equilibrium. But if variant 1 is favoured by direct and indirect biases (other lines) then it can overcome its benefit disadvantage and establish itself at a higher equilibrium frequency than variant 2. (d) Influence of strong conformity on the spread dynamic of six variants.

favours high-diversity situations where several invented variants are evenly distributed, innovation through improvement leads to a broader distribution of low and intermediate levels of diversity where the most beneficial variant shows a high frequency. The 95% limits of both distributions (where 5% of the probability mass is in the inner tail) indicate that diversity values between 0 and 0.48 can reasonably be attributed to innovation through modification whereas diversity values in the interval  $[0.72, 1]$  almost certainly result from independent invention. Thus for most of the range of values of this metric it should potentially be plausible to infer the process underlying innovation with a 5% probability of error. Fig. 3b illustrates the same situation but under the presence of a conformist bias which will be discussed in the next section.

#### 4. Social learning biases

We now model adoption behaviour in more detail by allowing for cultural transmission biases that favour particular variants, exploiting a general formulation devised by Henrich (2001) to capture several transmission biases simultaneously. Here, the adoption rate  $a$  is modelled by the function  $a = a(u) = (1-p)b + p(u - c_b)$  (Henrich, 2001) and analogously the switch rate  $c$  by the

function  $c = c(u) = [(1-p)d - p(u - c_b)]^+$ , where the operator  $[\cdot]^+$  stands for the positive part to ensure that the direction of switching is not changed. In both formulations we can clearly distinguish between a constant and a frequency-dependent component. The constant, or frequency-independent, components  $(1-p)b$  and  $(1-p)d$  represent the collective influence of direct bias (the selective copying of pre-existing variants found to be efficacious by individual assessment) and indirect bias (the selective copying of variants from individuals with specific qualities and attributes deemed to make them fit models), with  $b$  and  $d$  reflecting the population's judgement of the advantageousness of the variant given its intrinsic qualities, and those of its users. The frequency-dependent component  $p(u - c_b)$  represents the influence of a conformist bias (individuals preferentially adopt the commonest variant). If the variant's frequency  $u$  is above a 'commonness threshold'  $c_b$  then the difference  $u - c_b$  is positive and conformist bias results in an increase in the adoption rate and a decrease in the switch rate (adopters of a common variant are less likely to switch their variant), while if a variant is rare then conformity will reduce its adoption rate and increase its switch rate. The parameter  $p$  is a measure of the relative strength of the frequency-dependent and

frequency-independent components. Following Henrich (2001), we assume  $p$  is small.<sup>7</sup>

Fig. 4a illustrates the effects of different degrees of conformity on the spread dynamic of a single variant. Increasing conformity (either by incrementing  $p$  or the ‘commonness threshold’,  $c_b$ ) produces a delay in the take off of the adoption curve and, at the extreme, can hinder a variant from spreading altogether (yellow line). Fig. 4b illustrates the effects of conformity on the spread dynamic of a two-variant system where in each of four cases (represented by four colours) the dashed line is the more beneficial variant. A moderate level of conformity leads to an enhancement of variant 2’s advantage because conformist bias favours the common variant (compare blue to red lines). But if the population’s propensity for conformity is too large the dynamic is reversed (compare green or yellow to red lines), and strong support of the common variants prevents the more advantageous but later-invented variant 2 from spreading. This implies that strong conformity can hinder cumulative cultural evolution, resulting in a suboptimal equilibrium. When conformity is operating, the order in which the innovations occur and time between innovations play critical roles in determining which equilibrium will be reached. Fig. 4c illustrates the influences of frequency-independent bias on the spread of two variants. Where variant 1 is favoured by biases (blue and green lines) it can overcome its competitive disadvantage and establish itself at a higher equilibrium frequency than variant 2.

More generally, in an  $n$ -variant situation, low levels of conformity support the most beneficial variant, with its equilibrium frequency increased compared with unbiased learning, and a corresponding reduction in cultural diversity. In the presence of stronger conformist bias (Fig. 4d), less beneficial, and sometimes beneficial, variants are prevented from spreading, as a result of which cultural diversity decreases further. With high conformity, only one variant, which need not be the most beneficial variant, is present in the population. However, given the evidence in the historical and archaeological record for cumulative cultural evolution, we judge conformity of this magnitude to be implausible.

The effects of transmission biases hold for both innovation through modification and independent invention. When we consider the relationship between innovation rate and cultural diversity at equilibrium in the presence of moderate conformity, we again find that this relationship is both linear and positive. The effect of the conformist bias is both to reduce the absolute levels of diversity, and to increase the slopes of the diversity measures in the modification situation. As stated above, for innovation through modification evenness increases with the number of variants. However, here conformity can have a greater impact on situations with fewer variants, which is what leads to the larger slope of the diversity measures. While previously we proposed that high levels of cultural diversity may be indicative of independent invention whereas low levels might imply innovation through modification, in the presence of conformity this distinction is fuzzier. Fig. 3b shows the frequency distributions across the full range of diversity values for the Shannon index. Compared with the situation without conformity (Fig. 3a), with conformity the peaks of the distributions are now at the opposed ends of the diversity scale. Innovation through improvement most likely leads to situations where almost only one variant is dominant in the population. In contrast, the frequency distribution obtained by independent invention shows a multiple peak pattern. This pattern is indicative of situations where different numbers of dominant variants are supported.

<sup>7</sup> We note that a high degree of conformity can even lead to a negative intrinsic growth. The coefficient  $a_i(u_i)$  is interpreted as growth propensity which depends on the benefits a variant conveys to its adopters. If there is a very strong conformist bias acting in the population the conveyed benefit is largely determined by the variant’s frequency. Individuals may even discard originally beneficial but rare variants.

However, our analysis suggests that strong conformity is unlikely to be widespread in human culture. Boyd and Richerson (1985), Richerson and Boyd (2005) and their collaborators (e.g. Henrich and Boyd (1998), Henrich (2001), Henrich and McElreath (2003), McElreath et al. (2005) and Efferson et al. (2007)) have consistently placed emphasis on conformist transmission as an important mechanism of cultural evolution, stressing the evidence for conformity found in the social psychology literature (Ash, 1952; Coultas, 2004), and emphasizing the theoretical finding that conformity is favoured by selection over a broad range of conditions (Henrich and Boyd, 1998). However, this emphasis has recently received criticism from other cultural evolutionist theoreticians, whose analysis reveals that conformity hinders cumulative cultural evolution, and as a consequence would be selected against in many circumstances (Eriksson et al., 2007). These differences have yet to be resolved, but relate in part to different assumptions about patterns of environmental variation, and the cumulative or non-cumulative nature of cultural change. Our finding that a strong conformist bias can hinder the spread of a beneficial variant can be viewed as supporting Eriksson et al.’s (2007) argument that natural selection will not favour conformity if it prevents cumulative cultural evolution. Conversely, our observation that weak conformity typically increases the frequency of the most beneficial variant at equilibrium can be viewed as consistent with Henrich and Boyd’s (1998) conclusion that selection will favour conformity over a broad range of circumstances. Our analysis therefore contributes to this debate by emphasizing that the strength of conformity is likely to be a key issue. To the extent that human cultural change can be regarded as manifestly cumulative (Ghirlanda and Enquist, 2007), we anticipate that any conformist transmission is likely to be comparatively weak. If this reasoning proves correct the circumstances depicted in Fig. 3b are likely to be implausible, leaving the prospects for using the level of cultural diversity to infer the form of innovation favourable even in cases where weak conformity operates.

## 5. Summary

Our analysis leads to the following conclusions.

- The introduction of new variants typically increases cultural diversity substantially in the short term, but may actually decrease diversity, depending on the frequency of existing variants, and on how diversity is measured. Significant rates of innovation are required for innovation to reliably increase diversity.
- Innovation through modification can generate oscillating trends in diversity, when each variant is an improvement on the previous variants. Provided there is sufficient average time between innovations for the most beneficial variants to reach high frequency, a cycling pattern of diversity will emerge. In such circumstances, increasing trends towards greater average diversity are observed for medium but not low innovation rates, and high rates of innovation generating a steady increase in diversity. Conceivably, such oscillations may have utility as a signature of innovation through modification.
- Independent invention generally supports higher levels of cultural diversity than modification and refinement. Innovation through modification increases with innovation rate more rapidly than innovation through independent invention.
- While equilibrium levels of cultural diversity typically increase with innovation rate, this increase can be surprisingly modest, particularly when innovation occurs through refinements of earlier variants, or when conformist social learning is operating. A doubling of the innovation rate is typically associated with an increase in long-term cultural diversity of 6%–32%.

- Cultural diversity can be used as an indicator of whether the innovation process is driven by modification and refinement of existing variants or independent invention.
- Conformity weakens the relationship between innovation and diversity. Low levels of diversity enhance the equilibrium frequency of beneficial variants, but high levels of conformity may prevent beneficial variants from spreading. Only weak conformist transmission is likely to be favoured by selection.

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### Appendix A

The proposed model can be written as a general reaction–diffusion competition model where the time- and space-dependent variable  $K$  describes the size of the considered population and the variables  $u_i$  the time- and space-dependent relative frequencies of the different variants of the considered cultural trait within the population. Their spread patterns are modelled by the following  $(n + 1)$ -variant competition system:

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= d_1 \Delta u_1 + a_1 u_1 \left(1 - \frac{u_1}{K(t) - Z_1}\right) - \mu u_1 \\ &\quad - \sum_{i=2}^n c_{1i}(u_1) u_1 u_i + \sum_{i=2}^n c_{i1}(u_i) u_1 u_i + f_1(t, x), \\ \frac{\partial u_2}{\partial t} &= d_2 \Delta u_2 + a_2 u_2 \left(1 - \frac{u_2}{K(t) - Z_2}\right) - \mu u_2 \\ &\quad - \sum_{i=1, i \neq 2}^n c_{2i}(u_2) u_2 u_i + \sum_{i=1, i \neq 2}^n c_{i2}(u_i) u_2 u_i + f_2(t, x), \\ &\vdots \\ \frac{\partial u_n}{\partial t} &= d_n \Delta u_n + a_n u_n \left(1 - \frac{u_n}{K(t) - Z_n}\right) - \mu u_n \\ &\quad - \sum_{i=1}^{n-1} c_{ni}(u_n) u_n u_i + \sum_{i=1}^{n-1} c_{in}(u_i) u_n u_i + f_n(t, x), \\ \frac{\partial K(t)}{\partial t} &= (\lambda - \mu) K(t) (1 - K(t)), \end{aligned}$$

with  $Z_i = \sum_{k=1, k \neq i}^n u_k$  and the boundary conditions

$$\frac{\partial u_i}{\partial n} = 0, \quad \text{for } x \in \partial D, i = 1, \dots, n.$$

These boundary conditions describe the situation for a finite environment (a bounded convex two-dimensional domain  $D$ ), with no diffusion possible beyond its boundary  $\partial D$ . This assumption would be fulfilled if we imagine  $D$  as isolated by natural barriers, preventing exchange with the wider world. The general growth behaviour of the considered population is modelled by the last equation. It is assumed that the growth follows a bounded logistic pattern where  $\lambda$  and  $\mu$  stand for the birth respectively death rates of the population. Further, the terms  $\partial u_i / \partial t$  indicate the temporal changes of the variant frequencies and it is assumed that these changes are determined by a diffusion and a growth component. The diffusion component is modelled by the terms  $d_i \Delta u_i$  which describe the spatially spread of the variants through unbiased social learning (or asocial learning) based on a random walk with density-dependent mixing. The coefficients  $d_i$  describe the ‘diffusion coefficients’ and are measures of the scale of

spatial interaction within the population. The growth components are given by the reaction terms  $a_i u_i \left(1 - \frac{u_i}{K(t) - Z_i}\right) - \mu u_i - \sum_{k=1, k \neq i}^n c_{ik}(u_i) u_i u_k + \sum_{k=1, k \neq i}^n c_{ki}(u_k) u_i u_k$  and can be attributed to three different sources, intrinsic growth, death, and competition. The intrinsic growth captures the process by which naive individuals adopt a specific variant without knowing about the alternative variants. This process is modelled by  $a_i u_i \left(1 - \frac{u_i}{K(t) - Z_i}\right)$ , which describes bounded logistic growth with the growth rate  $a_i$  and the additional assumption that the variants  $u_i$  are mutually exclusive variants of the considered trait. We associate the rate  $a_i$  with the population’s judgement of the benefit of a specific variant  $i$ . The more ‘useful’ a variant is to individuals in the population the faster it can increase in frequency. In our analysis we consider  $a_i > 0$ , which means that all variants are beneficial to some degree, although the degrees of benefit can be different. Our assumption of mutually exclusive variants implies that the sum of the variant frequencies has to be restricted to the population size  $K(t)$  which characterizes the state where the whole population has adopted one of the possible variants of the considered cultural trait. That can be expressed by the condition

$$\sum_{i=1}^n u_i(t, x) \leq K(t), \quad \text{for any time } t \text{ and any location } x,$$

and it follows that the growth process of each variant is restricted by the size of the ‘naive’ population  $K(t) - Z_i$ . The term  $\mu u_i$  models the loss of adopters of each variant due to natural death and we assume that the fraction  $\lambda u_i$  of newborns enters the population as ‘naive’ individuals who may, depending on the intrinsic growth coefficients  $a_i$  and the frequencies of the variants in the considered area, adopt one of the present variants. Further, the presence of different variants in the population causes competition and the growth is influenced by individuals that have already adopted a variant switching to an alternative variant. Here we take the symmetrical approach that the loss of adopters of variant  $i$  (due to the presence of variant  $j$ ) results in the gain of variant  $j$  and vice versa. These interactions between the variants are described by the competition terms  $c_{ij}(u_i) u_j u_i$ , which model the switching processes from variant  $i$  to variant  $j$ . If we rewrite the terms

$$c_{ij}(u_i) u_j u_i = \bar{c}_{ij}(u_i, u_j) u_i,$$

they can be interpreted as a reduction of the intrinsic growth behaviour due to the presence of the other variant. The switching rates  $\bar{c}_{ij}(u_i, u_j)$  are determined by the number of adopters of the competing variant,  $u_j$ , and the general attitude towards the switching of both variants,  $c_{ij}(u_i)$ . The exact form of this function has to be derived from the specific application. Here we use an approach where the attitude is dependent on the variant’s frequency to account for the fact that some individuals might not want to switch from their (already beneficial) variant to another variant for various reasons. For instance, there is archaeological evidence that not all hunters and gatherers convert into farmers (Layton et al., in press). Finally, we assume that the variants do not have to be present at the beginning ( $t = 0$ ), but can be invented at later time points. We model the invention points by an exponential distributed random variable,

$$\tau \sim \exp(\lambda),$$

which describes the time between two innovations. The use of the exponential distribution is motivated by the fact that innovation during a certain time period can be described as a Poisson process. This stochastic process assumes that the events occur with an average rate  $\lambda$  and independently and it is known that the time between successive Poisson events is exponential distributed with the same intensity  $\lambda$ . The parameter  $\lambda$  stands for the rate of



innovation. The process of innovation is modelled by the functions  $f_i$ . If the invention of variant  $i$  occurs,  $f_i$  is non-zero in a small area and for a small period of time so that the variant  $i$  becomes present in the population.

We implemented the model in C++ and solved it numerically with the Finite Element Method.

## Appendix B

In order to quantify cultural diversity we use four diversity measures which we develop through borrowing related biodiversity, species richness and evenness measures from biology.

### B.1. Simpson index

In a finite population the Simpson index represents the probability that two randomly selected individuals in the habitat carry different variants. It takes into account the number of variants present, as well as the relative abundance of each variant. Since we deal with continuous frequency variables we use the formulation

$$D_1 = 1 - \sum_{i=1}^n p_i^2, \quad \text{with } p_i = \frac{\int_D u_i(t, x) dx}{\sum_{k=1}^n \int_D u_k(t, x) dx}. \quad (1)$$

The terms  $p_i$  define the relative frequency of variant  $i$  in the population and  $D_1$  describes the probability that two randomly chosen individuals carry different variants. It yields  $0 \leq D_1 \leq (n-1)/n$ , where values near  $(n-1)/n$  correspond to highly diverse systems and values near zero to more homogeneous systems.

### B.2. Shannon index

The Shannon index incorporates the number of variants present as well as their abundance. It is defined by

$$D_2 = - \sum_{i=1}^n p_i \ln p_i,$$

where  $p_i$  defines the relative frequency of variant  $i$  in the population (cp. relation (1)). This index corresponds to the entropy measures in information theory or thermodynamics. It is increasing either by having more unique variants, or by having a greater variant evenness, but is not standardized to 1. Standardization leads to the evenness index given by

$$D_3 = \frac{D_2}{\ln n},$$

where the denominator  $\ln n$  describes the maximal value of the Shannon index  $D_2$ . The evenness index quantifies how equal the variants are numerically.

### B.3. Bulla index

Bulla (1994) pointed out that the above indices are little influenced by the abundance of rare variants and are not able to distinguish between situations which differ only in the presence or absence of rare variants. He proposed an index that evaluates the size of the overlapping area of the frequency distribution in a completely even situation where all variants have the same frequencies and the empirical distribution. The index can be written as

$$D_4 = \frac{\sum_{i=1}^n \min(p_i, 1/n) - 1/n}{1 - 1/n},$$

where  $n$  represents the number of variants which are present in the population and so the quotient  $1/n$  represents the frequency of each variant in a completely homogeneous situation. It is analogue to  $D_3$  an evenness index.

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