

The pace of modern culture

Ben Lambert¹, Georgios Kontonatsios², Matthias Mauch³, Theodore Kokkoris⁴,
Matthew Jockers⁵, Sophia Ananiadou² and Armand M. Leroi^{6,7*}

Here we investigate the evolutionary dynamics of several kinds of modern cultural artefacts—pop music, novels, the clinical literature and cars—as well as a collection of organic populations. In contrast to the general belief that modern culture evolves very quickly, we show that rates of modern cultural evolution are comparable to those of many animal populations. Using time-series methods, we show that much of modern culture is shaped by either stabilizing or directional forces or both and that these forces partly regulate the rates at which different traits evolve. We suggest that these forces are probably cultural selection and that the evolution of many artefact traits can be explained by a shifting-optimum model of cultural selection that, in turn, rests on known psychological biases in aesthetic appreciation. In sum, our results demonstrate the deep unity of the processes and patterns of cultural and organic evolution.

Modern culture appears to change very quickly. New art objects, scientific results and technologies arise all the time. Some flourish, others wither, but all are sooner or later replaced by something else. On the basis of this ceaseless flux, many have claimed that human culture evolves much more quickly than organisms do^{1–4}. Since ideas are transmitted much more quickly among minds than genes are among bodies, we might even expect artefact phenotypes to evolve much more faster organismal ones; however, there is little empirical reason to believe this.

This is because the relative rate of biological and cultural evolution is a quantitative issue, and whereas the rate of biological evolution has often been estimated^{5–9}, the rate of cultural evolution has not. To our knowledge, only one study—based on archaeological artefacts⁴—has attempted a direct comparison between rates of biological and cultural evolution. We, however, are interested in modern culture, the province of historians. Although historians often make claims about relative rates of evolution—such as when they argue for the existence of periods of stagnation or revolution in the arts, science or technology—they invariably do on the basis of purely qualitative evidence (for example, in refs. ^{10–16}). Even major monographs that take an explicitly evolutionary view of technological change are entirely devoid of graphs (for example, refs. ^{17–21}). To our knowledge, no major history of the poetry, painting or pottery of any era or nation contains quantitative estimates of rates of change of any kind.

Recently, the availability of large collections of digital artefacts—texts, images and music—and computational methods to quantify their properties, have permitted the quantitative study of modern culture^{22–26}. Here we use such data and methods to directly compare the dynamics of organic and cultural evolution and the forces that shape them. We study four classes of modern cultural artefacts: popular music, novels, clinical literature and cars, as well as a variety of evolving animal populations. Applying rate metrics developed by evolutionary biologists^{5–9}, we show that cultural artefacts do not generally evolve faster than animal populations. We then investigate the forces that regulate them. Inspired by studies of organic fossils^{6,7,27–32}, we investigate whether any given trait is subject to

directional or stabilizing forces, or whether it evolves as an unbiased random walk. We find that most cultural and organic traits are indeed subject to such forces; about a quarter of traits show mean-reverting dynamics, that is, stasis. Finally, we investigate whether these forces influence their relative long-term rates of evolution. We show that, while both directional and stabilizing forces do so, the stabilizing forces are more influential than the directional forces. In short, the reason why a large part of modern culture shows so little long-term change is because of the action of some constraining force.

In this study, we view each class of artefact: songs, novels, clinical papers and cars, as a population. This forms the basis of our comparison between the evolution of artefacts and living things. Dobzhansky³³ defined a population as “a reproductive community of sexual and cross-fertilizing individuals which share in a common gene pool”; that is, as a unit of evolution³⁴. Since assemblages of artefacts do not literally reproduce or have sex, it may seem that they cannot be populations in Dobzhansky’s sense. However, contrary to appearances, they can and are. This is because when we make a new artefact such as a scientific paper, poem or pot, we are invariably influenced by existing artefacts, often combining their features in some new way and sometimes even adding genuinely new features¹⁸. The analogy of cultural transmission to genetic inheritance, complete with recombination and mutation, has long been noted^{3,35–37}. An assemblage of artefacts is, in this view, directly analogous to a population of sexually reproducing organisms in that the creation of a new entity entails not only the transmission of design information, but its exchange.

Archaeologists have, accordingly, analysed the evolution of arrowheads and pottery shards in a similar way to how palaeontologists have analysed evolving populations of organisms^{38,39}. When doing so, they rightly treat every individual artefact as a unique entity⁴. The products of modern culture, however, differ from those of pre-modern societies in that they are of two kinds: intentionally unique designs and mechanically or digitally produced copies that are essentially identical to their models⁴⁰. Since we want to compare the evolutionary dynamics of modern artefacts to those

¹Department of Infectious Disease Epidemiology, Faculty of Medicine, Imperial College London, London, UK. ²National Centre for Text Mining, Manchester Institute of Biotechnology, University of Manchester, Manchester, UK. ³School of Electronic Engineering and Computer Science, Queen Mary University of London, London, UK. ⁴Department of Computing, Imperial College London, London, UK. ⁵College of Arts and Sciences, Washington State University, Pullman, WA, USA. ⁶Department of Life Sciences, Imperial College London, London, UK. ⁷Data Science Institute, Imperial College London, London, UK.

*e-mail: a.leroi@imperial.ac.uk

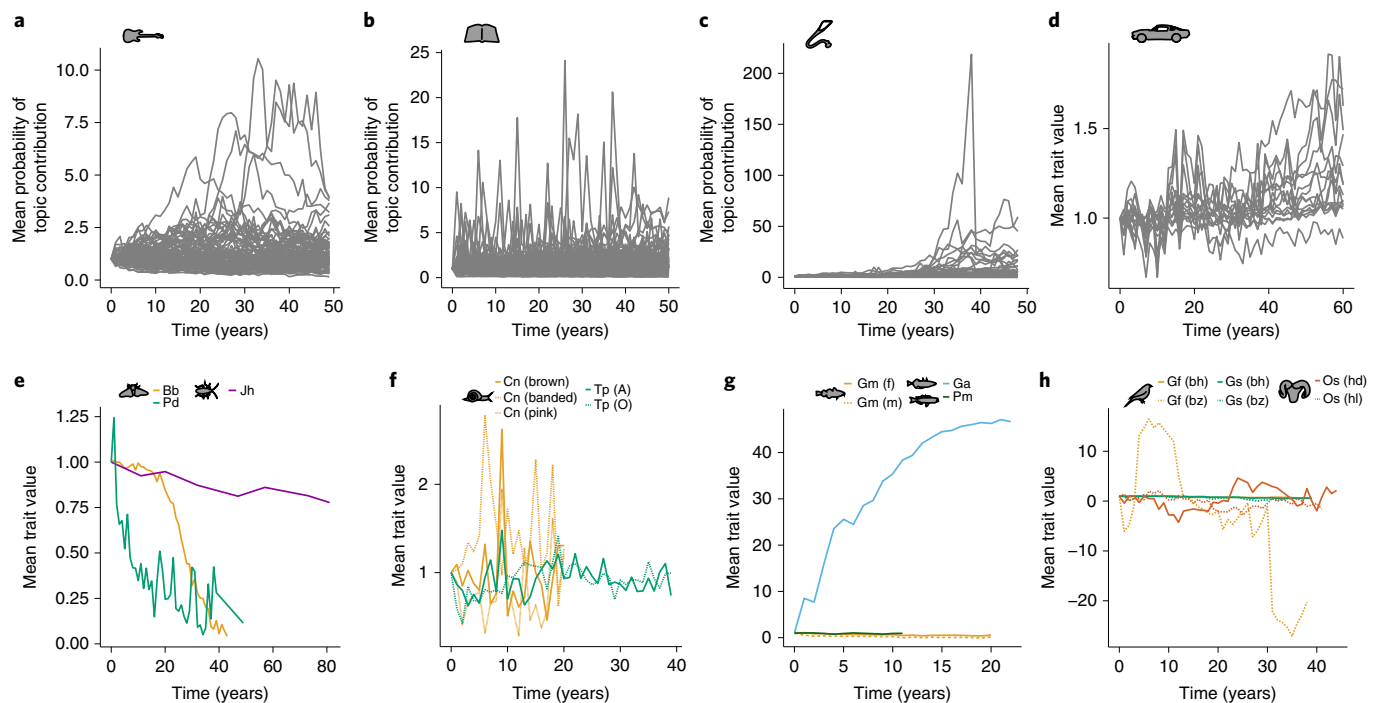


Fig. 1 | Evolutionary trajectories of artefact and organic populations. **a**, Pop music: US Billboard Hot 100 from 1960 to 2010. **b**, English, Irish and American novels from 1840 to 1890. **c**, Clinical literature: *British Medical Journal* from 1960 to 2008. **d**, Fossil fuel-powered cars sold in the USA from 1950 to 2010. For pop music, novels and the clinical literature, each line represents the mean probability that a given topic contributes to the documents or songs of that year. For pop music, we used 100 topics; for novels, we used 476 topics; and for clinical literature, we used 73 topics. The car traits are 16 powertrain and body-size traits. **e**, Organic populations: Bb, *B. betularia* frequency of *carbonaria* morph in Caldys, UK, 1959 to 2002; Pd, *P. dominula* frequency of *medionigra* morph in Cothill, UK, 1939 to 1988; Jh, *Jadera haematoloma* beak length in Florida, 1898 to 1979. **f**, Cn, *C. nemoralis* frequencies of banded, brown and pink morphs in Fyfield Down, UK, 1964 to 1984; Tb, *Theba pisana* frequencies of effectively banded morph in acacia (A) and open (O) habitat in Bold Park, Western Australia, 1977 to 2016. **g**, Ga, *Gasterosteus aculeatus* frequency of low plate morph in Lake Loberg, USA, 1991 to 2012; Gm, *Gadus morhua* age at maturity—females (f) and males (m)—in Scotian Shelf, North Atlantic, 1959 to 1980; Pm, *Perissodus microlepis* frequency of sinistral morph in Lake Tanganyika, Democratic Republic of the Congo, 1980 to 1991. **h**, *Geospiza fortis* (Gf) and *G. scandens* (Gs) beak size (bz) and shape (bh) in Daphne Minor, Galapagos, 1973 to 2012; Oc, *Ovis canadensis* horn length (hl) and diameter (hd) in Ram Mountain, Canada, 1963 to 2012. For clarity, each trait has been standardized so that $\bar{z}_0 = 1$. Note that the scales of the axes vary among plots. See Supplementary Table 1 for sources of the organic population data.

of sexually reproducing organisms, it is clear that we should only attend to the former. Thus, our populations are based on the set of unique designs: unique songs, novels, medical paper and car models, and not the copies they engendered. Millions may have watched Gangnam Style on YouTube or driven a Toyota Corolla, but both get counted only once. We also suppose that each artefact class is indeed a single population rather than a complex of related ‘species’. By this we mean that, when designing a new artefact, artists, writers, engineers and scientists can, in principle, be influenced by the design of any extant artefact of the same class; that the most divergent artefacts—for example, a country song and a rap song—might be combined to make something new. The ubiquity of ‘cross-over’ genres, a marketing term with apt, if surely unintentional, echoes of genetic recombination, shows the unity of our classes: country-rap or hick-hop actually exists. Scientific papers also comprise a single population, but their divergent cross-over products are generally called ‘interdisciplinary’; this paper is an example of one.

Our artefact populations are then as follows: the songs that entered the US Billboard Hot 100 between 1960 and 2010; American, Irish and English novels published between 1840 and 1890; the articles published in the *British Medical Journal* from 1960 to 2008; and car models sold in the USA between 1950 and 2010. Our samples of these populations (see Methods) consist of 17,094 unique songs²⁶, 2,203 novels that were collected by the Stanford Literary Lab in 2011⁴¹, 170,577 clinical articles and 2,210 car models. For pop music, clinical articles and car models, these samples

comprise at least 80% of the population; for novels our sample is an unknown, but much smaller, fraction of the population. Our pop music, novel and medical paper traits are topic probabilities⁴², which may be thought of as discrete traits that capture the content of a song or document; our car traits are sixteen powertrain and body-size traits. These traits are replicative units whose frequencies or values can be tracked over time, and thus we view them as transmissible units sensu⁴³. Our organic populations include some of the most famous long-term studies of animal evolution in the wild, such as a 50-year long study of the scarlet tiger moth *Panaxia dominula* in Oxfordshire, England⁴⁴, a 43-year long study of the peppered moth *Biston betularia* in northwest England⁴⁵, a 40-year long study of Darwin’s finches in the Galapagos islands⁴⁶, and a 20-year long study of the snail *Cepaea nemoralis* in Wiltshire, England⁴⁷. In all, our organic dataset is based on the phenotypes of 301,694 individuals. Note that the studied populations, as defined above, are not necessarily a random sample of all potentially interbreeding individuals. For example, we do not have data on the many pop songs that never charted, nor the many *Geospiza scandens* finches that did not live on Daphne Minor.

Results

Cultural evolution and organic evolution slow down over longer intervals. Fig. 1 shows the evolutionary trajectories of the traits assayed in these populations. Since the temporal resolution of the series, their length and scales of measurement all vary, their relative

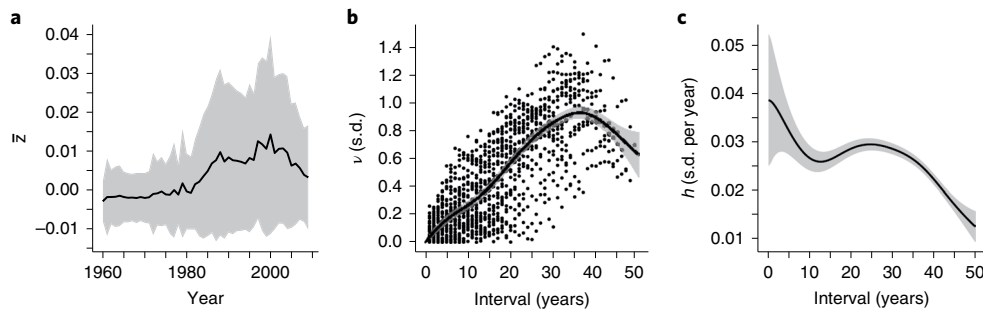


Fig. 2 | Estimating Haldane rates from time series. a–c, The evolutionary trajectory of a pop music topic is shown as its mean presence in the songs of a given year, \bar{z}_i ; the ribbon indicates ± 1 s.d. (**a**). The means and s.d. for each year are used to compute the Haldane numerator, ν_i , for all intervals permitted by the data (points); yearly estimates of $\bar{\nu}_i$ (line) and their 95% confidence intervals (ribbon) are then obtained by fitting a general additive model (**b**). The Haldane rates, h_i , and their 95% confidence intervals are then computed by dividing $\bar{\nu}_i$ by the interval, I (**c**).

rates of evolution cannot be determined by simply looking at them. To compare rates of evolution, biologists have developed several metrics^{5,6}. Here we use Haldanes because this metric accounts for within-population variation, and as Haldane himself wrote, variation is the raw material of evolution. Ideally, this metric is normalized using the generation time to account for different time scales of evolution. However, we do not have generation times for our artefacts, and it is unclear how to estimate them. For this reason, we calculate Haldanes for all traits using a common time scale, years, that is easily interpreted. In an evolving population sampled at times t_1 and t_2 with phenotypic means \bar{z}_1 and \bar{z}_2 of a trait, the Haldane (h), is the rate of change per unit of time over the interval $I = t_2 - t_1$, calibrated in standard deviations:

$$h = \frac{(|\bar{z}_2 - \bar{z}_1|)/S}{t_2 - t_1} = \frac{|\Delta\bar{z}|/S}{I} \quad (1)$$

where S is the pooled sample standard deviation, calculated from the sample standard deviations s_1 and s_2 and n_1 and n_2 , the sample sizes, at the two time points:

$$S = \frac{s_1 \cdot (n_1 - 1) + s_2 \cdot (n_2 - 1)}{(n_1 + n_2 - 2)} \quad (2)$$

The quantity $\nu = |\Delta\bar{z}|/S$ is known as the Haldane numerator.

Given a dataset of points \bar{z}_i and their standard deviations s_i (Fig. 2a), we are interested in finding the Haldane rates h_i that encapsulate the rate of evolution over any interval I . First, for all pairs of time points t and $t - I$ permitted by the data, we calculate the raw Haldane numerators ν_{it} and bucket them by interval I (Fig. 2b). A robust estimate $\bar{\nu}_i$ is then obtained by fitting a general additive model. Finally, as illustrated in Fig. 2c, we use this estimate to calculate:

$$h_i = \bar{\nu}_i / I \quad (3)$$

This method enables us to estimate and compare Haldane rates over a particular interval^{16,48} and is similar to the method recommended by Kinnison and Hendry⁹, who suggest using segmented linear regression. Both their method and ours avoid the auto-correlation that arises from modelling h_i , which contains I in its denominator, as a function of I (refs. ^{9,49,50}). Since we have no a priori ideas about the direction of evolution, we estimate absolute rates of evolution.

Studies of organic populations have shown that rates of evolution slow down as interval sizes increase^{6–9,51}; we found that artefact traits also exhibit this pattern (Fig. 3). We also found this pattern in many of our organic populations, even though our data are based on time series of individual populations rather than, as is usual, point estimates of divergence in an arbitrary collection of populations. Our results are not a consequence of the auto-correlation between h_i and I , since our method of estimating Haldane rates does not depend on modelling these two parameters as a function of each other.

The slowing in the rate of evolution with increasing interval implies that, over the long term, most traits are much more conservative than one would naively expect from observing the annual fluctuations of their means. For example, in an average pop music trait, all phenotypic shifts may be in the same direction. If its h_1 rate was constant over all intervals, then after fifty years of evolution, its mean will have shifted by nearly two standard deviations. In fact, its mean shifts by only 0.005 standard deviations—around 0.25% of what it would have done had the rate of evolution been constant over all I . This may explain why, for all the flux of artists, songs and styles through the charts, new pop songs rarely seem very unfamiliar.

The decline in rates of evolution with interval also mean that if we are to compare rates of evolution, we must do so for particular intervals. We therefore focused on the year-to-year absolute Haldane rate, h_1 , which describes short-term changes in population means, and its 25-year equivalent, h_{25} , which describes long-term changes. We find that, from one year to the next, cars evolve about 1.3 times faster than novels, 3.6 times faster than pop music and 8.1 times faster than the clinical literature. This rank order remains true over 25-year intervals, but the differences in rate are slightly smaller (Figs. 3a–d and 4a,b). Since the number of topics, k , sought in a population is arbitrary, we examined the impact of varying k on our results, but found that the rank order of the Haldane rates among our populations was preserved regardless of whether we used a hundred topics or a thousand (Supplementary Fig. 1).

Modern culture and animals evolve at similar rates. We next estimated rates in our organic populations. Previous studies have estimated rates of evolution by combining point estimates of divergences from many different populations^{6–9,27,31}, but we wanted to investigate individual trait rate dynamics, and thus focused on those with good time-series data.

Overall, we found that h_1 varies by more than an order of magnitude in these animal populations (Fig. 3e–h and Supplementary Table 2). The fastest evolving animal populations involved polymorphic traits. These traits involve two or more alternative morphs or phenotypes that may be present in a population; for example,

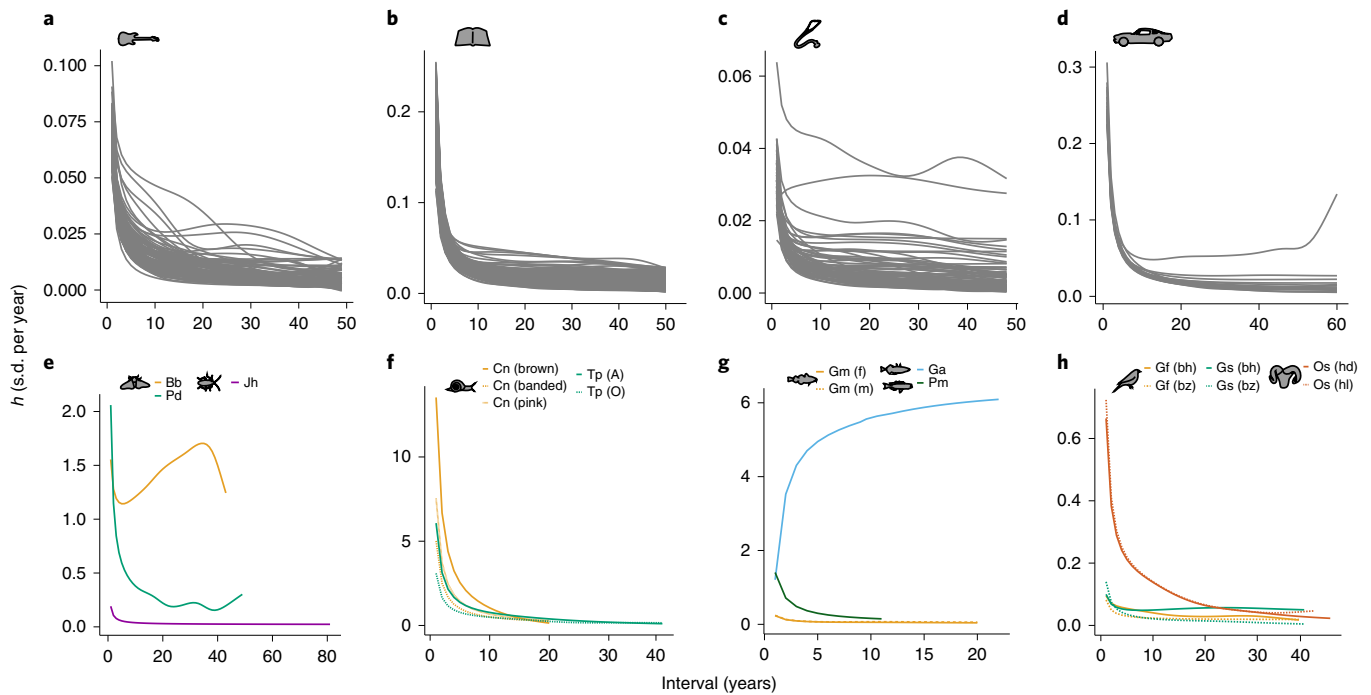


Fig. 3 | Rates of evolution of artefact and organic populations. a–h, Rates of evolution in absolute Haldanes (h) of artefact and organic populations. Populations as in Fig. 1. Note that the scales of the axes vary among plots.

the white and melanistic *carbonaria* morphs of *B. betularia* in Cald, near Manchester. For this species, the melanistic *carbonaria* morph—a classic case of directional evolution driven by natural selection⁴⁵—evolved at a rate of $h_1 = 1.56$ s.d. per year (Figs. 1 and 3e), but snail shell colour polymorphisms, which fluctuate greatly in frequency from one year to the next, evolved at a rate of $h_1 > 3$ s.d. per year. The highest long-term rate of evolution was found in the three-spined stickleback, *G. aculeatus*, of Loberg lake, Alaska⁵², whose armour plating evolved at a rate of $h_{22} = 6.0$ s.d. per year. Because these rates are much higher than most published estimates of rates of organic evolution, we also applied the log rate–log interval method^{6,7,51} and found very similar results (Supplementary Fig. 2). All our polymorphic traits showed h_1 rates in excess of 0.7 s.d. per year, regardless of whether they were evolving directionally or not.

Our data also include several sets of continuous traits, the most well known of which are from Peter and Rosemary Grant's study of Darwin's finches, *G. fortis* and *G. scandens*, in the Galapagos^{46,53} (Figs. 1 and 3h). Compared with polymorphisms, continuous traits had low h_1 rates (Supplementary Table 2). Only two traits had $h_1 > 0.2$ s.d. per year: age at maturity in Atlantic cod and horn size in bighorn sheep, both of which were subject to strong fishing or hunting pressure^{54–56}.

Polymorphisms are due to alleles at a few loci and are under strong genetic control, meaning that their Haldane rates are true rates of evolution. By contrast, changes in continuous traits may be caused partially, or even entirely, by phenotypic plasticity (for example, in refs. 57,58), so their Haldane rates are properly viewed as rates of phenotypic change. Whereas genetic studies confirm that the observed change in each of our continuous traits is partially heritable^{46,53,55,59,60}, we view them as upper bounds on rates of evolution.

How do rates of artefact and organic evolution compare? Biologists have long been keen to demonstrate evolution in action, and many of these populations were studied precisely in the hope that they might do so. For this reason, our data are surely not representative of organic traits in general. They do, however, suggest

upper limits to the rate of organic evolutionary change. Notably, the upper limits of the distribution of h_1 for all four artefact distributions are well below the upper limits of the distribution of organic traits (Fig. 4a,c and Supplementary Table 3). This is mostly due to our inclusion of polymorphisms, which have generally been ignored in compilations of evolutionary rates^{6,8,9}; however, even if we exclude them, it is clear that the upper limits of cultural and organic traits are of the same order of magnitude, $0.1 < h_1 < 1.0$ s.d. per year. This is also true whether we consider vertebrate or invertebrate species alone. We have fewer 25 year interval data for organic populations, but again no artefact trait has a h_{25} greater than the most rapidly evolving organic trait (Fig. 4b,d). Hunt has shown²⁹ that, even in the absence of evolution, Haldane rates have a small but finite value due to sampling error, which may dominate when sample sizes are small. The lower bounds of the estimated Haldane confidence intervals of most of our traits, however, exceed this minimum value, at least in the long term (Supplementary Fig. 3); that is, our traits have evolved. We conclude that rates of cultural and organic evolution are surprisingly comparable and that some organic traits can evolve much faster than any cultural trait we observed.

Although we focused on populations and traits with time-series data, we did consider some point estimates of evolutionary rates available in the literature. We were particularly interested in a study on guppies evolving in response to a novel predation pressure⁶¹, because the observed rates in Darwins were said to be very high, and, importantly, were based on animals raised in a common garden and so reflect genuine evolutionary change. The highest rate in these guppies ($h_4 = 0.26$ s.d. per year for male age to maturity in El Cedro river fish) is about 4.5 times faster than the fastest Darwin's finch beak trait over comparable intervals, but slower than those of many polymorphisms. We also reanalysed a dataset based on point estimates of phenotypic change in 49 different species and traits⁶² and found that the mean Haldane rate was $\bar{h}_{\leq 4} = 0.08$ s.d. per year. The fastest evolving trait in this dataset was a morphometric trait in a population of sticklebacks from Iceland, where $h_1 = 0.71$ s.d. per year (Supplementary Table 4).

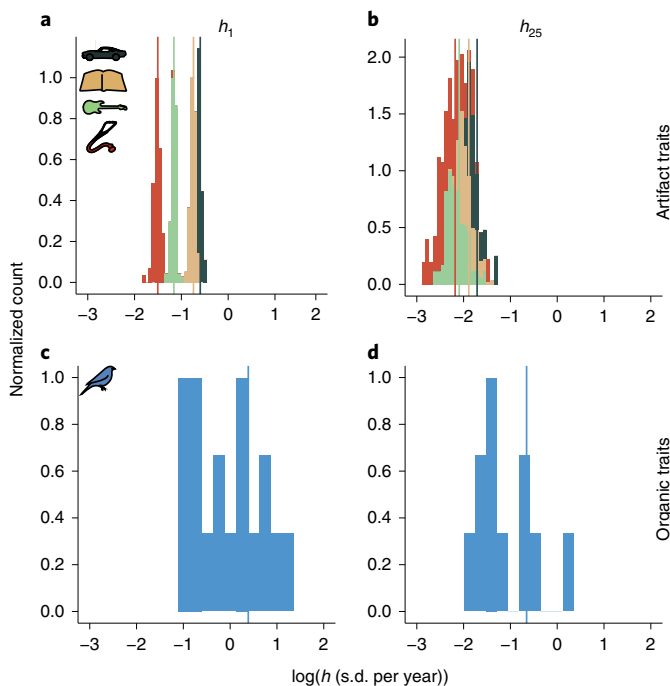


Fig. 4 | Distribution of Haldane rates for cultural and organic traits.

a,b, Cultural traits: pop songs (green guitar), novels (brown book), clinical literature (red stethoscope) and cars (black car). **c,d**, Organic traits (blue bird). Year-to-year Haldane rates, $\log(h_1)$ (**a,c**); long-term Haldane rates, $\log(h_{25})$ (**b,d**). Vertical lines are medians.

Why rates of evolution vary. We have shown that the long-term rate of evolution (h_{25}) of both cultural and organic traits varies greatly: some change swiftly where others are more conservative. Can we explain this variation? In organic sexual populations, the rate of fixation of novel variants is a function of effective population size, the mutation rate and the form and magnitude of selection⁶³. This is also true for cultural traits, except that the intergenerational sorting of variants is often labelled ‘transmission biases’ of various sorts rather than selection^{35,64–66}. Since we do not know the values of these parameters for any of our traits, it may seem that we cannot hope to explain why some evolve more quickly than others. However, we can quantify, at a more abstract level, some of the forces that shape them.

We begin by observing that, in the absence of any other forces, a trait will evolve as an unbiased random walk (URW). For a URW, the expected value of a trait in the next generation equals its current value. By contrast, if it is subject to stabilizing forces, the trait will show reversion to the mean or, if subject to directional forces, a directional trend^{67–69}. These patterns suggest two explanations for the variation in the long-term rate of evolution. Conservative traits may be subject to stabilizing forces, whereas fast-evolving traits may be less so, meaning the latter evolve as random walks. Alternatively, conservative traits may be random walks (with small variance per time step) whereas fast-evolving traits are driven by directional forces. Thus, all else being equal and assuming additivity, mean-reverting, unbiased random-walk and directionally evolving traits have increasingly rapid rates of long-term evolution. We now consider whether these forces are acting on our traits.

Series that are the result of URW and mean-reverting processes will show interval-dependent rate declines of the type seen in Fig. 3, albeit with different magnitudes; directional biased series will not show such declines^{49,50} (see Supplementary Fig. 4 for simulations showing this effect). Indeed, the pattern of interval dependence of

rates has been proposed as a way to test for the presence of these forces⁵¹, but such tests have been criticized as weak⁷⁰. Since we have longitudinal data, we estimated the directional and stabilizing forces acting on each of our traits using time-series analysis. To do this, we adopted a two-step procedure. First we asked whether each trait was a mean-reverting process or a general random walk. Of note, the outcome of this step does not determine whether the series has a directional trend, since a process can be mean-reverting about a trend, or can be a biased random walk (BRW), a process whose mean changes with time. As such, we then determined whether each trait had a directional trend. The result of this procedure is a fourfold classification of our evolutionary trajectories as URW, BRW, unbiased mean-reverting (UMR) and biased mean-reverting (BMR) processes.

To distinguish between mean-reverting and general random walks we estimated the persistence (ρ) of each trait in the population. Specifically, we estimated an AR1 process, an autoregressive process in which the current value is based on the immediately preceding value, for each trait mean $\bar{z}(t)$ of the form:

$$\bar{z}(t) = \rho \bar{z}(t_1) + \epsilon(t) \quad (4)$$

where $\epsilon \sim \mathcal{N}(0, \sigma)$, and the process exhibits mean-reversion if $\rho < 1$. Within each population, such as pop music, the traits will probably be related due to their common origins. To account for this dependence between traits, we estimated a Bayesian hierarchical model for each different population. In our Bayesian hierarchical model, we allow ρ to vary across different traits within a population, although the individual parameters are drawn from a common population-level distribution of the form:

$$\rho(z) \sim \mathcal{N}(\bar{\rho}, \tau) \quad (5)$$

where z indicates the trait, τ is the s.d. of the population-level distribution, and $\bar{\rho}$ is the population mean of ρ . If, for some trait, the 95th percentile of the posterior distribution of $\rho < 1$, we classified it as mean-reverting and as a general random walk if not.

We distinguished between traits showing directional evolution and those that did not by estimating, for each trait in each population, the bias in its trend, δ . Since random walks are, by their nature, non-stationary time series, we mitigated against the risk of spurious results by estimating a model of the form:

$$\Delta \bar{z}(t) = \delta + \epsilon(t) \quad (6)$$

where $\Delta \bar{z}(t) = \bar{z}(t) - \bar{z}(t-1)$ is the first difference operator. Whereas, if the trait was mean-reverting, we estimated:

$$\bar{z}(t) = \delta t + \epsilon(t) \quad (7)$$

If, for some trait, the 5th and 95th percentiles of the posterior distribution of δ did not overlap zero, we classified it as biased; otherwise it was classed as unbiased.

Using this classification we found that most artefact traits showed directional or mean-reverting dynamics or both: only between 0% and 16% of the traits, depending on the population, were URWs (Table 1). This was also true of organic traits, but in this case 22% (4 out of 18) of the traits, were URWs. The traits of our four artefact populations varied in their average persistence. On average, clinical literature traits were closest to random walks, with a typical trait drawn from the population having $\rho = 0.89 \pm 0.11$ (mean estimate \pm s.d.), followed by pop music traits ($\rho = 0.78 \pm 0.10$), cars ($\rho = 0.63 \pm 0.26$) and novels ($\rho = 0.51 \pm 0.22$). Surprisingly, between 25% and 86% of artefact traits, depending on population, and 44%

(8 out of 18) of organic traits showed both directional and BMR dynamics, suggesting that many cultural and organic traits are shaped by some stabilizing force pushing trait values towards a mean that is itself evolving under some directional force.

Given these results, we can now ask how much variation in the long-term rate of evolution (h_{25}) can be explained by directional forces as measured by bias (δ), stabilizing forces as measured by persistence (ρ), and population-specific properties. Considering all 659 cultural traits in a single linear model, we found that ρ , δ , population and their second-order interactions each explain statistically significant amounts of the variance in h_{25} , 85% in all. Of the two continuous variables, the interaction of ρ and population explained about three times as much of the variance as the interaction of δ and population (see Supplementary Table 5 for analysis of variance and Supplementary Table 6 for relative importance estimates). We also modelled h_{25} as a function of ρ and δ separately for each population and found similar results (Fig. 5a, inset table). These results imply that for any given population of artefacts, the main reason that some traits are relatively conservative is because they are constrained by particularly strong stabilizing forces, but directional selection also has a role. Since in our global model, much of the variance in h_{25} is explained by population and its interaction with ρ and δ , neither directional nor stabilizing forces, by themselves, explain differences in the average rate of evolution of populations. This implies that differences in effective population sizes, mutation rates or else sampling effects also contribute. This is also true of our organic populations (not shown).

Discussion

Our aim in this study is to lay the empirical foundations of a science of history that embraces both living things and artefacts. To that end, we began by comparing rates of organic and cultural evolution. In pre-modern societies, cultural evolution can appear very slow. Words in related languages can remain obvious cognates despite thousands of years of divergence⁷¹; even technological artefacts, such as the Japanese sword, can remain unchanged for centuries⁷². More surprisingly, we show that modern culture also evolves slowly—in general, no faster than animals do.

This result may seem inconsistent with a recent study showing that the year-on-year rate of evolution of archaeological artefacts is about 50% faster than that of organic traits⁴. Methodological differences prevent a direct comparison between that study and ours, but we note that the earlier study did not consider many of the most rapidly evolving organic populations that we do and so may underestimate the rate of organic evolution. Although we have studied several different kinds of artefacts, it seems certain that some technologies—or at least some of their properties—must evolve more quickly than organisms do. Moore's law⁷³ is not a distribution-based rate and so is not comparable to the rates that we report here; even so, a 24 month doubling time of maximum transistor density surely implies that the population of extant computers evolves faster than even the most briskly evolving animal populations. Indeed, if we had data on the computing power rather than horsepower of modern cars, it is possible that we would have found a dimension of car performance that outpaces even stickleback lateral plates.

Are the ever-changing properties of pop songs, novels, the clinical literature and cars—and all the other human-made things that fill our world—merely a matter of chance, or are they shaped by various forces? The question is a familiar one, for it lies at the heart of many disciplines that consider how populations composed of diverse entities change over time. It has indeed been one of the central questions of cultural evolution^{74–80}, inherited from the dichotomy between neutralist and selectionist models in evolutionary biology^{68,81}. In community ecology, it appears as a similar dichotomy between neutral ecological theory and theories that seek to explain community dynamics in terms of the properties of species

Table 1 | Classifying cultural and organic traits according to their directionality and tendency to revert to a mean.

Population	URW	BRW	UMR	BMR
Pop music	0	0	26	74
Novels	1	0	20	79
Clinical literature	16	29	30	25
Cars	7	0	7	86
Animals	22	6	28	44

For each population or set of populations, we report the percentage of traits that we infer to be URW, BRW, UMR and BMR. Note that by unbiased and random walk, we mean those traits in which we have failed to detect a bias or mean-reversion, respectively. See text for how this classification was constructed.

and their niches^{82,83}; in economics, it appears as the tension between efficient markets and investment value accounts of stock market movements^{84,85}. Moreover, the kind of data we have collected, and the time-series methods we have applied to answer this question, have also been used by evolutionary biologists, ecologists and economists^{68,86,87}, reflecting the deep similarities between these fields and the phenomena they consider.

We have distinguished four kinds of processes that might underlie the evolution of a trait: URW, BRW, UMR and BMR. The last three of these imply the existence of forces that shape the mean or—in the case of a discrete trait—its frequency, either pushing it in a particular direction or else pulling it towards an equilibrium value, or both. To put this another way, rejection of a URW in favour of these alternatives implies that the evolution of the trait in question is not neutral but depends on the value of its mean or frequency at any time. Recently, several studies have reported tests of the neutrality of various cultural traits such as first names, pottery and academic vocabulary. Where some have claimed that their evolution can be explained by random copying giving rise to cultural drift^{74–77,79,88}, others claim evidence for various biases^{78,80,89,90}. Consistent with the latter, we find that the evolution of most cultural traits are the result of either biased or mean-reverting processes, implying that much of modern culture is shaped by either directional or stabilizing forces. These forces also largely explain why some traits of a given class of artefacts evolve faster than others.

What might these forces be? By analogy with biology, the most obvious force is cultural selection: by producers—the people who make the artefacts, gatekeepers—the people who distribute and sell them, or consumers—the people who buy and use them⁹¹. By cultural selection, we mean any process by which one cultural trait is more likely to be acquired and transmitted than another, a definition that includes various transmission biases^{3,35,36} and cultural attractors^{92–97}. Our discovery of widespread mean-reversion and its influence on the long-term rate of evolution in cultural traits is particularly interesting, for stasis has long preoccupied evolutionary biologists who have sought to explain why many recent and fossil populations evolve so slowly when even modest selection has the power to change them so quickly^{27,31,32,68,98}. Many biologists, when considering continuous traits, have favoured stabilizing selection as the cause of stasis^{27,32,99,100}, or when considering polymorphisms, negative frequency dependent selection and heterosis^{101,102}. Others have emphasized that the direction of selection might fluctuate in time and so cancel out over the long run^{46,53,103–105} or, allowing that populations might be subdivided into smaller demes that remain connected by gene flow, that it might vary in direction across space to no net long-term effect¹⁰⁶.

It is notoriously difficult to unravel which of these various kinds of selection accounts for the stability of any given trait. The *Cepaea* shell colour polymorphisms, for example, are thought to be actively maintained, and our analysis confirms this, but decades of work

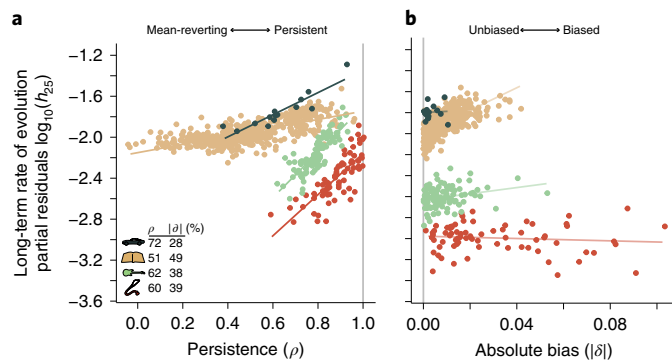


Fig. 5 | Why the long-term rate of evolution of culture varies. a,b, For our 659 cultural traits, we modelled the rate of evolution in Haldanes over 25-year intervals (h_{25}) as a function of two continuous variables estimated from time-series analyses—persistence and directional bias—as well as a categorical trait, the population to which they belong. We show the partial residuals of this model—that is, the trait values for each variable when the other is held constant at the population medians (**a,b**). Coloured lines give the least-squares fit. We also modelled h_{25} as a function of ρ and δ separately for each population. The inset table in **a** reports the fraction of the variance explained by ρ and δ , relative to the total variance explained by the main effects, when each population is modelled separately.

have led to the conclusion that many different stabilizing forces are at work at various temporal and spatial scales^{102,107}. Among the cultural traits that show stasis, that is, a consistently high average frequency and UMR dynamics (Supplementary Table 7), are pop music topics that capture smooth, harmonic, male or female vocals (for example, The Pussycat Dolls' Top Of The World (2009)) and those with loud guitar (for example, Lenny Kravitz's Fly Away (1998)). Novel topics that show stasis include those concerned with everyday subjects (travel, passion or dinner), crime (police, magistrates or evidence) and class distinctions (servants, fashion or hunting). Our data do not permit us to identify selective forces responsible for the stasis that we observe, but it is also true that culture is inherently less mysterious than snails. Including artists such as The Rolling Stones, The Ronettes, Lenny Kravitz and The Pussycat Dolls, pop music has always had a place for noisy, aggressive music with lots of drums and guitars as well as girl bands with smooth, rounded vocals. Since many of the books in the Stanford Literary Lab corpus are British and Irish, their concern with class distinctions and crime is not unexpected. Discounting the possibility that these topics are maintained by cultural mutation pressure alone—loud guitars do not require continual reinvention—it seems plausible that their perennial presence is due to negative frequency-dependent selection or, less abstractly, a steady demand in the pop music-listening and fiction-reading publics of the time, one that authors, songwriters, editors and producers actively sought to meet but not exceed. Demonstrating this, however, will require detailed studies analogous to studies of natural selection in the wild in which the relative success of cultural traits are directly measured.

We note two limitations of our study. First, as mentioned above, some technologies—or at least some of their properties—must evolve faster than organisms do. Indeed, it is the perpetual need to replace our mobile phones and update our operating systems that probably gives us the sense that human culture is evolving at a breakneck speed. Should data on the distribution of such technologies in the population—an assay of the phones and computers we actually own, rather than just the latest models—become available, it will be possible to compare their rates of evolution to those estimated here. Second, when estimating Haldane rates for any given interval (such as h_i), we obtained a single estimate over the entire

time series; yet rates of evolution can vary, for example, during punctuational changes or revolutions. Detecting such events, however, requires more complex models and different methods to those used here (such as those used in ref. 108).

One of our most striking results is the large fraction of cultural and organic traits that are both directional (biased) and mean-reverting. We suggest that these traits are subject simultaneously to both directional and stabilizing selection. Estes and Arnold²⁷, fitting macroevolutionary models to point estimates of divergence collected from many organic populations, argued that their data could be best explained by a 'shifting-optimum' model, and our results are consistent with this. One psychological mechanism that could generate a shifting optimum is if selective agents at any time continually favour an intermediate level of novelty, as captured by the Wundt–Berlyne curve of hedonic satisfaction^{109–111}.

The stability of topic 332—'servants of gentlemen'—in 19th century novels reminds us that, just as in organic populations, cultural equilibria do not last forever. Sudden changes in the environment or radical innovations can transform the space of evolutionary possibilities^{27,31,104}, what G. G. Simpson called the 'adaptive zone'¹¹². When cars no longer run on gasoline, the selective forces that have shaped the internal combustion engine for more than a century will also vanish. Moreover, while we have shown that, between 1960 and 2010, pop music topics 81 and 72—both of which capture loud guitars—were actively maintained by some force, it does not follow that rock and roll can never die.

Methods

Data. Pop music: we characterized the evolution of the US Billboard Hot 100 from 1960–2010 in terms of topic probabilities, each of which represents a combination of musical properties that capture some aspect of the harmonic and timbral qualities of the music. In previous work²⁶, we identified 8 harmonic and 8 timbral topics; here we identify 100 topics that combine harmonic and timbral properties. Clinical literature: We studied the *British Medical Journal* between 1960 and 2008, identifying 100 topics using latent Dirichlet allocation, which we filtered for those directly concerned with clinical practice or medical research using the words most highly associated with each topic, leaving us with 73 topics. Preliminary analysis showed extremely rapid increases in the means of a small number of topics in 1997 and early 1998 due to a temporary change in the journal's editorial policy, whereby each issue focused on a special subject; we removed these issues, leaving us with 170,577 documents. Novels: we used the Stanford Literary Lab corpus of 19th century novels, limiting it to those published between 1840 and 1890 to maximize annual sample size, leaving us with 2,203 documents. We identified 500 topics⁴¹, which we then filtered to remove uninterpretable or metadata topics leaving us with 471. Cars: we obtained data on the dimensions and powertrains of car models from <https://carqueryapi.com>. Models frequently exist as many variants, and many of those variants are updates. To allow for changes in the attributes of a given model over time, we summarized these variants by decade, giving 2,210 model–decade variants in all (for example, Toyota Corolla 1960, Toyota Corolla 1970,..., Toyota Corolla 2010). We then averaged the attributes of these model–decade variants to obtain a single estimate for each of 16 quantitative traits. We filtered the data to include only cars that could run on fossil fuels and were sold in the USA when new, between 1950 and 2010. Missing data were imputed using FactoMineR¹¹³ and missMDA packages in R¹¹⁴. For the artefact populations, each unique kind of artefact—song, article, novel or car model—is represented only once in the dataset, at the date of first appearance. Organic populations: we obtained data directly from researchers or otherwise, by digitizing figures; see Supplementary Information for references.

Topic analysis. For the pop music, novels and the clinical dataset, we extracted topics by latent Dirichlet allocation⁴² implemented in MALLET¹¹⁵. We performed hyperparameter optimization for every 10 Gibbs sampling iterations, setting the total number of iterations to 2,000.

Time-series analysis. The two steps of categorizing traits—the Bayesian hierarchical model of AR1 processes (Eq. (4),(5)), and the estimation of directional trends for the individual traits (equations (6) and (7))—were conducted in R, using the Stan package¹¹⁶ for the Markov chain Monte Carlo (MCMC). For each model, we ran 8 separate Markov chains, each for a total of 400 iterations, and discarded the first half of samples as the 'warm-up'. In each model, all the parameters satisfied $\hat{R} < 1.1$, giving an indication that the sampling distribution had converged to the posterior¹¹⁷.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data used in the study are available from <https://github.com/Armand1/Pace-of-Modern-Culture>.

Received: 11 March 2019; Accepted: 29 November 2019;

Published online: 20 January 2020

References

- Cronk, L. Intelligent design in cultural evolution. *Behav. Brain Sci.* **29**, 352–353 (2006).
- Richerson, P. J., Boyd, R. & Henrich, J. Gene–culture coevolution in the age of genomics. *Proc. Natl Acad. Sci. USA* **107**, 8985–8992 (2010).
- Mesoudi, A. *Cultural Evolution: How Darwinian Theory Can Explain Human Culture and Synthesize the Social Sciences* (Univ. Chicago Press, 2011).
- Perreault, C. The pace of cultural evolution. *PLoS One* **7**, e45150 (2012).
- Haldane, J. B. S. Suggestions as to quantitative measurement of rates of evolution. *Evolution* **3**, 51–56 (1949).
- Gingerich, P. D. Rates of evolution—effects of time and temporal scaling. *Science* **222**, 159–161 (1983).
- Gingerich, P. D. Quantification and comparison of evolutionary rates. *Am. J. Sci.* **293A**, 453–478 (1993).
- Hendry, A. P. & Kinnison, M. T. The pace of modern life: measuring rates of contemporary microevolution. *Evolution* **53**, 1637–1653 (1999).
- Kinnison, M. T. & Hendry, A. P. The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* **112**, 145–164 (2001).
- Kuhn, T. *The Structure of Scientific Revolutions* (Univ. Chicago Press, 1972).
- Rosen, C. & Zerner, H. *Romanticism and Realism* (Faber and Faber, 1984).
- Shapin, S. *The Scientific Revolution* (Univ. Chicago Press, 1996).
- Danto, A. C. *After the End of Art: Contemporary Art and the Pale of History* (Princeton University Press, 1997).
- Blanning, T. *The Romantic Revolution* (Weidenfeld & Nicholson, 2010).
- Wootton, D. *The Invention of Science: a New History of the Scientific Revolution* (Allen Lane, 2015).
- Heumakers, A. *De Esthetische Revolutie* (Boom, 2015).
- Mokyr, J. *The Lever of Riches: Technological Creativity and Economic Progress* (Oxford Univ. Press, 1992).
- Basalla, G. *The Evolution of Technology* (Cambridge Univ. Press, 1988).
- Ziman, J. (ed.) *Technological Innovation as an Evolutionary Process* (Cambridge Univ. Press, 2000).
- Steadman, P. *The Evolution of Designs: Biological Analogy in Architecture and the Applied Arts* (Cambridge Univ. Press, 2008).
- Arthur, W. *The Nature of Technology: What It Is and How It Evolves* (Allen Lane, 2009).
- Michel, J. B. et al. Quantitative analysis of culture using millions of digitized books. *Science* **331**, 176–182 (2011).
- Serrà, J., Corral, A., Bogaña, M., Haro, M. & Arcos, J. L. I. Measuring the evolution of contemporary western popular music. *Sci. Rep.* **2**, 521 (2012).
- Hughes, J. M., Foti, N. J., Krakauer, D. C. & Rockmore, D. N. Quantitative patterns of stylistic influence in the evolution of literature. *Proc. Natl Acad. Sci. USA* **109**, 7682–7686 (2012).
- Rodriguez Zivic, P. H., Shifres, F. & Cecchic, G. A. Perceptual basis of evolving western musical styles. *Proc. Natl Acad. Sci. USA* **110**, 10034–10038 (2013).
- Mauch, M., MacCallum, R. M., Levy, M. & Leroi, A. M. The evolution of popular music: USA 1960–2010. *R. Soc. Open Sci.* **2**, 150081 (2015).
- Estes, S. & Arnold, S. J. Resolving the paradox of stasis: models with stabilizing selection explain evolutionary divergence on all timescales. *Am. Nat.* **169**, 227–244 (2007).
- Hunt, G. Evolution in fossil lineages: paleontology and the origin of species. *Am. Nat.* **176**, S61–S76 (2010).
- Hunt, G. Measuring rates of phenotypic evolution and the inseparability of tempo and mode. *Paleobiology* **38**, 351–373 (2012).
- Hunt, G., Hopkins, M. J. & Lidgard, S. Simple versus complex models of trait evolution and stasis as a response to environmental change. *Proc. Natl Acad. Sci. USA* **112**, 4885–4890 (2015).
- Uyeda, J. C., Hansen, T. F., Arnold, S. J. & Pienaar, J. The million-year wait for macroevolutionary bursts. *Proc. Natl Acad. Sci. USA* **108**, 15908–15913 (2011).
- Arnold, S. J. Phenotypic evolution: the ongoing synthesis. *Am. Nat.* **183**, 729–746 (2014).
- Dobzhansky, T. Mendelian populations and their evolution. *Am. Nat.* **84**, 401–418 (1950).
- Hey, J. Regarding the confusion between the population concept and Mayr's population thinking. *Q. Rev. Biol.* **86**, 253–264 (2011).
- Cavalli-Sforza, L. L. & Feldman, M. W. *Cultural Transmission and Evolution: a Quantitative Approach*. (Princeton Univ. Press, 1981).
- Boyd, R. & Richerson, P. J. *Culture and the Evolutionary Process* (Univ. Chicago Press, 1985).
- Mesoudi, A., Whiten, A. & Laland, K. N. Is human cultural evolution Darwinian? Evidence reviewed from the perspective of the origin of species. *Evolution* **58**, 1–11 (2004).
- O'Brien, M. J. & Lyman, R. L. *Applying Evolutionary Archaeology: a Systematic Approach* (Springer, 2000).
- Mesoudi, A. & O'Brien, M. J. The cultural transmission of Great Basin projectile-point technology I: an experimental simulation. *Am. Antiq.* **73**, 3–28 (2008).
- Benjamin, W. *Illuminations: Essays and Reflections* (Schocken, 1969).
- Jockers, M. *Macroanalysis: Digital Methods and Literary History* (Univ. Illinois Press, 2013).
- Blei, D. M., Ng, A. Y. & Jordan, M. I. Latent Dirichlet allocation. *J. Mach. Learn. Res.* **3**, 993–1022 (2003).
- O'Brien, M. J., Lyman, R. L., Mesoudi, A. & VanPool, T. L. Cultural traits as units of analysis. *Philos. Trans. R. Soc. B* **365**, 3797–3806 (2010).
- Jones, D. A. 50 years of studying the scarlet tiger moth. *Trends Ecol. Evol.* **4**, 298–301 (1989).
- Cook, L. M. The rise and fall of the carbonaria form of the peppered moth. *Q. Rev. Biol.* **78**, 399–417 (2003).
- Grant, P. R. & Grant, B. R. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* **296**, 707–711 (2002).
- Cain, A. J., Cook, L. M. & Currey, J. D. Population size and morph frequency in a long-term study of *Cepaea nemoralis*. *Proc. R. Soc. B* **240**, 231–250 (1990).
- Kurten, B. Rates of evolution in fossil mammals. *Cold Spring Harb. Symp. Quant. Biol.* **24**, 205–215 (1959).
- Sheets, H. & Mitchell, C. Uncorrelated change produces the apparent dependence of evolutionary rate on interval. *Paleobiology* **27**, 429–445 (2001).
- Roopnarine, P. Analysis of rates of morphologic evolution. *Annu. Rev. Ecol. Syst.* **34**, 605–632 (2003).
- Gingerich, P. D. Rates of evolution. *Annu. Rev. Ecol. Syst.* **40**, 657–675 (2009).
- Bell, M. A. & Aguirre, W. E. Contemporary evolution, allelic recycling, and adaptive radiation of the threespine stickleback. *Evol. Ecol. Res.* **15**, 377–411 (2013).
- Grant, P. R. & Grant, B. R. *40 Years of Evolution: Darwin's Finches on Daphne Major Island* (Princeton Univ. Press, 2014).
- Beacham, T. Variability in median size and age at sexual maturity of Atlantic cod, *Gadus morhua*, on the Scotian shelf in the Northwest Atlantic Ocean. *Fish. Bull.* **81**, 303–321 (1983).
- Coltman, D. W. et al. Undesirable evolutionary consequences of trophy hunting. *Nature* **426**, 655–658 (2003).
- Pigeon, G., Festa-Bianchet, M., Coltman, D. W. & Pelletier, F. Intense selective hunting leads to artificial evolution in horn size. *Evol. Appl.* **9**, 521–530 (2016).
- Seeley, R. Intense natural selection caused a rapid morphological transition in a living marine snail. *Proc. Natl Acad. Sci. USA* **83**, 6897–6901 (1986).
- Trussell, G. & Smith, L. Induced defenses in response to an invading crab predator: an explanation of historical and geographic phenotypic change. *Proc. Natl Acad. Sci. USA* **97**, 2123–2127 (2000).
- Olsen, E. et al. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* **428**, 932–935 (2004).
- Carroll, S. et al. And the beak shall inherit—evolution in response to invasion. *Ecol. Lett.* **8**, 944–951 (2005).
- Reznick, D. N., Shaw, F. H., Rodd, F. H. & Shaw, R. G. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* **275**, 1934–1937 (1997).
- Gotanda, K. M., Correa, C., Turcotte, M. M., Rolshausen, G. & Hendry, A. P. Linking macroevolution and microevolution: re-evaluating microevolutionary support for Cope's rule. *Evolution* **69**, 1345–1354 (2015).
- Kimura, M. & Ohta, T. The average number of generations until fixation of a mutant gene in a finite population. *Genetics* **61**, 763–771 (1969).
- Henrich, J. Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses: the Tasmanian case. *Am. Antiq.* **69**, 197–214 (2004).
- Aoki, K., Lehmann, L. & Feldman, M. W. Rates of cultural change and patterns of cultural accumulation in stochastic models of social transmission. *Theor. Popul. Biol.* **79**, 192–202 (2011).
- Nakashishi, W. The effect of cultural interaction on cumulative cultural evolution. *J. Theor. Biol.* **352**, 6–15 (2014).
- Hunt, G. Fitting and comparing models of phyletic evolution: random walks and beyond. *Paleobiology* **32**, 578–601 (2006).
- Hunt, G. The relative importance of directional change, random walks, and stasis in the evolution of fossil lineages. *Proc. Natl Acad. Sci. USA* **104**, 18404–18408 (2007).

69. Hunt, G. & Rabosky, D. L. Phenotypic evolution in fossil species: pattern and process. *Annu. Rev. Earth Planet. Sci.* **42**, 421–441 (2014).
70. Sheets, H. & Mitchell, C. Why the null matters: statistical tests, random walks and evolution. *Genetica* **112**, 105–125 (2001).
71. Pagel, M., Atkinson, Q. D. & Meade, A. Frequency of word-use predicts rates of lexical evolution throughout Indo-European history. *Nature* **449**, 717 (2007).
72. Martin, G. in *Technological Innovation as an Evolutionary Process* (ed. Ziman, J.) Ch. 8 (Cambridge Univ. Press, 2000).
73. Moore, G. E. Cramming more components onto integrated circuits. *Electronics* **38**, 114–117 (1965).
74. Shennan, S. & Wilkinson, J. Ceramic style change and neutral evolution: a case study from neolithic europe. *Am. Antiq.* **66**, 577–593 (2001).
75. Hahn, M. & Bentley, R. Drift as a mechanism for cultural change: an example from baby names. *Proc. R. Soc. B* **270**, S120–S123 (2003).
76. Bentley, R., Hahn, M. & Shennan, S. Random drift and culture change. *Proc. R. Soc. B* **271**, 1443–1450 (2004).
77. Bentley, R. A., Lipo, C. P., Herzog, H. A. & Hahn, M. W. Regular rates of popular culture change reflect random copying. *Evol. Hum. Behav.* **28**, 151–158 (2007).
78. Lycett, S. J. Acheulean variation and selection: does handaxe symmetry fit neutral expectations? *J. Archaeol. Sci.* **35**, 2640–2648 (2008).
79. Bentley, R. A., Ormerod, P. & Shennan, S. Population-level neutral model already explains linguistic patterns. *Proc. R. Soc. B* **278**, 1770–1772 (2011).
80. Acerbi, A. & Bentley, R. A. Biases in cultural transmission shape the turnover of popular traits. *Evol. Hum. Behav.* **35**, 228–236 (2014).
81. Lynch, M. The rate of morphological evolution in mammals from the standpoint of the neutral expectation. *Am. Nat.* **136**, 727–741 (1990).
82. Hubbell, S. P. *The Unified Neutral Theory of Biodiversity and Biogeography* (Princeton Univ. Press, 2001).
83. Rosindell, J., Hubbell, S. P., He, F., Harmon, L. J. & Etienne, R. S. The case for ecological neutral theory. *Trends Ecol. Evol.* **27**, 203–208 (2012).
84. Fama, E. F. Efficient capital markets: a review of theory and empirical work. *Finance* **25**, 383–417 (1970).
85. Piotroski, J. D. Value investing: the use of historical financial statement information to separate winners from losers. *J. Account. Res.* **38**, 1–41 (2000).
86. Poterba, J. M. & Summers, L. H. Mean reversion in stock prices: evidence and implications. *J. Financ. Econ.* **22**, 27–59 (1988).
87. Lo, A. W. *Adaptive markets: Financial Evolution at the Speed of Thought* (Princeton, 2017).
88. Bentley, R. A. Random drift versus selection in academic vocabulary: an evolutionary analysis of published keywords. *PLoS One* **3**, e3057 (2008).
89. Brantingham, P. J. & Perreault, C. Detecting the effects of selection and stochastic forces in archaeological assemblages. *J. Archaeol. Sci.* **37**, 3211–3225 (2010).
90. Crema, E. R., Kandler, A. & Shennan, S. Revealing patterns of cultural transmission from frequency data: equilibrium and non-equilibrium assumptions. *Sci. Rep.* **6**, 39122 (2016).
91. MacCallum, R. M., Mauch, M., Burt, A. & Leroi, A. M. Evolution of music by public choice. *Proc. Natl Acad. Sci. USA* **109**, 12081–12086 (2012).
92. Sperber, D. *Explaining Culture* (Blackwell, 1996).
93. Sperber, D. & Hirschfeld, L. A. The cognitive foundations of cultural stability and diversity. *Trends Cogn. Sci.* **8**, 40–46 (2004).
94. Claidière, N. & Sperber, D. Imitation explains the propagation, not the stability of animal culture. *Proc. R. Soc. B* **277**, 651–659 (2010).
95. Claidière, N., Kirby, S. & Sperber, D. Effect of psychological bias separates cultural from biological evolution. *Proc. Natl Acad. Sci. USA* **109**, E3526–E3526 (2012).
96. Leroi, A. M., MacCallum, R. M., Mauch, M. & Burt, A. Reply to Claidière et al.: Role of psychological bias in evolution depends on the kind of culture. *Proc. Natl Acad. Sci. USA* **109**, E3527–E3527 (2012).
97. Claidière, N., Scott-Phillips, T. & Sperber, D. How Darwinian is cultural evolution? *Philos. Trans. R. Soc. B* **369**, 1471–297 (2014).
98. Gould, S. J. *The Structure of Evolutionary Theory* (Harvard Univ. Press, Cambridge, MA, 2002).
99. Charlesworth, B., Lande, R. & Slatkin, M. A neo-Darwinian commentary on macroevolution. *Evolution* **36**, 474–498 (1982).
100. Charlesworth, B. & Lande, R. Morphological stasis and developmental constraint—no problem for neo-Darwinism. *Nature* **296**, 610 (1982).
101. Bond, A. B. The evolution of color polymorphism: crypticity searching images, and apostatic selection. *Annu. Rev. Ecol. Syst.* **38**, 489–514 (2007).
102. Cook, L. M. Selection and disequilibrium in *Cepaea nemoralis*. *Biol. J. Linn. Soc.* **108**, 484–493 (2013).
103. Stanley, S. & Yang, X. Approximate evolutionary stasis for bivalve morphology over millions of years—a multivariate, multilineage study. *Paleobiology* **13**, 113–139 (1987).
104. Bell, G. Fluctuating selection: the perpetual renewal of adaptation in variable environments. *Philos. Trans. R. Soc. B* **365**, 87–97 (2010).
105. Bergland, A., Behrman, E., O'Brien, K., Schmidt, P. & Petrov, D. Genomic evidence of rapid and stable adaptive oscillations over seasonal time scales in *Drosophila*. *PLoS Genetics* **10**, e1004775 (2014).
106. Hendry, A., Day, T. & Taylor, E. Population mixing and the adaptive divergence of quantitative traits in discrete populations: a theoretical framework for empirical tests. *Evolution* **55**, 459–466 (2001).
107. Jones, J., Leith, B. & Rawlings, P. Polymorphism in *Cepaea*: a problem with too many solutions? *Annu. Rev. Ecol. Syst.* **8**, 109–143 (1977).
108. Leroi, A. et al. On revolutions. *Palgrave Commun.* (in the press).
109. Berlyne, D. Novelty, complexity, and hedonic value. *Percept. Psychophys.* **8**, 279–286 (1970).
110. Berlyne, D. E. *Aesthetics and Psychobiology* (Appleton-Century-Crofts, 1971).
111. Sreenivasan, S. Quantitative analysis of the evolution of novelty in cinema through crowd sourced keywords. *Sci. Rep.* **3**, 2758 (2013).
112. Simpson, G. G. *Tempo and Mode in Evolution* (Columbia Univ. Press, 1944).
113. Lê, S., Josse, J. & Husson, F. FactoMineR: an R package for multivariate analysis. *J. Stat. Softw.* **25**, 1–18 (2008).
114. Josse, J. & Husson, F. missMDA: a package for handling missing values in multivariate data analysis. *J. Stat. Softw.* **70**, 1–31 (2016).
115. McCallum, A. K. *MALLET: a Machine Learning for Language Toolkit* (Univ. Massachusetts, 2002).
116. Carpenter, B. et al. Stan: a probabilistic programming language. *J. Stat. Softw.* **76**, 1–32 (2017).
117. Gelman, A. & Rubin, D. B. Inference from iterative simulation using multiple sequences. *Stat. Sci.* **7**, 457–472 (1992).

Acknowledgements

We thank A. Burt, G. Bell, L. Cook, D. Coltman, P. Grant, K. Gotanda, M. Fortelius, A. Hendry, M. Johnson, G. Pigeon and M. Pagel for data, advice or comments on the manuscript. The authors received no specific funding for this work.

Author contributions

B.L. and A.M.L. designed the study, carried out analysis and wrote the paper. G.K., M.M., M.J. and S.A. supplied data and carried out analysis. T.K. supplied data.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at <https://doi.org/10.1038/s41562-019-0802-4>.

Correspondence and requests for materials should be addressed to A.M.L.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Primary handling editors: Charlotte Payne and Aisha Bradshaw

© The Author(s), under exclusive licence to Springer Nature Limited 2020

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see [Authors & Referees](#) and the [Editorial Policy Checklist](#).

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a Confirmed

- ☐ ☒ The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
- ☐ ☒ A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- ☐ ☒ The statistical test(s) used AND whether they are one- or two-sided
Only common tests should be described solely by name; describe more complex techniques in the Methods section.
- ☐ ☒ A description of all covariates tested
- ☐ ☒ A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
- ☐ ☒ A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- ☐ ☒ For null hypothesis testing, the test statistic (e.g. F , t , r) with confidence intervals, effect sizes, degrees of freedom and P value noted
Give P values as exact values whenever suitable.
- ☐ ☒ For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- ☐ ☒ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- ☐ ☒ Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

Data collection Standard R packages were used

Data analysis Standard R and STAN packages were used

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research [guidelines for submitting code & software](#) for further information.

Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

All data will be made publicly available

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

- ☐ Life sciences ☒ Behavioural & social sciences ☐ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://www.nature.com/documents/nr-reporting-summary-flat.pdf)

Behavioural & social sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	phenotypic data on assemblages of cultural artefacts and various organic species over time
Research sample	species data: temporal data on the phenotypes of 10 species. cultural data: the songs that entered the U.S. Billboard Hot 100, 1960–2010; American, Irish, and English novels published between 1840 and 1890; the articles published in the British Medical Journal, 1960–2008; car models sold in the USA, 1950–2010. Our samples of these populations consist of 17,094 unique songs ²⁷ , 2,203 novels that were collected by the Stanford Literary Lab in 2011 ⁴² , 170,577 clinical articles and 2,210 car models.
Sampling strategy	The species data were obtained from the literature, the sampling strategy is unique to each study and generally unknown. The cultural data were mostly collected by us. For pop music, clinical articles and car models, these samples comprise at least 80% of the study population; for novels our sample is an unknown, but much smaller, fraction of the population.
Data collection	NA
Timing	NA
Data exclusions	no data excluded
Non-participation	NA
Randomization	NA

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology
<input checked="" type="checkbox"/>	<input type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Human research participants
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data

Methods

n/a	Involved in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging