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A systems approach to cultural evolution

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ABSTRACT A widely accepted view in the cultural evolutionary literature is that culture forms a dynamic system of elements (or 'traits') linked together by a variety of relationships. Despite this, large families of models within the cultural evolutionary literature tend to represent only a small number of traits, or traits without interrelationships. As such, these models may be unable to capture complex dynamics resulting from multiple interrelated traits. Here we put forward a systems approach to cultural evolutionary research—one that explicitly represents numerous cultural traits and their relationships to one another. Basing our discussion on simple graph-based models, we examine the implications of the systems approach in four domains: (i) the cultural evolution of decision rules ('filters') and their influence on the distribution of cultural traits in a population; (ii) the contingency and stochasticity of system trajectories through a structured state space; (iii) how trait interrelationships can modulate rates of cultural change; and (iv) how trait interrelationships can contribute to understandings of inter-group differences in realised traits. We suggest that the preliminary results presented here should inspire greater attention to the role of multiple interrelated traits on cultural evolution, and should motivate attempts to formalise the rich body of analyses and hypotheses within the humanities and social science literatures.

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Introduction

Research in cultural evolution aims at understanding and explaining cultural change at multiple causal levels (e.g., Mesoudi, 2011; Colleran and Mace, 2015; Gjesfjeld et al., 2016). Culture, like many targets in science, is complex, with multiple processes interacting at a variety of spatial and temporal scales. This is evident both in the multiple definitions of culture, many of which selectively highlight features and processes of culture and cultural change (Kroeber and Kluckhohn, 1952; Weiss, 1973; Keesing, 1974; Mesoudi, 2011), and in the variety of methods used to decompose and analyse the constituent causal processes of culture.[1] Despite variation among these attempts at describing and understanding the complexity of human culture, there has long been consensus on its key features: that culture is composed of a number of distinct elements (or traits), that these traits bear varying relationships to one another, and that these traits are realised in overlapping yet heterogeneous ways by different populations in the world.

In calling this a consensus, we draw attention to the long history of viewing culture as a complex dynamic system, composed of multiple traits and their relationships, which can change over time. This is a view arguably as old as the discipline of anthropology itself: clear precursors of such thinking can be found in the writings of British sociocultural evolutionists (Stocking, 1987) and the various schools of nineteenth century German anthropology (Smith, 1991). This consensus view persisted in the works of twentieth century American evolutionary anthropologists (Carneiro, 2003), as well as in anthropology's interpretivist, structuralist, and post-structuralist traditions (Kuper, 1999). More relevant for current considerations, this consensus view is also evident in the qualitative descriptions accompanying early cultural evolutionary models (e.g., Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985) and in banner claims about the scope and power of cultural evolutionary theory (e.g., Sperber, 1996; Henrich, 2016).

Nonetheless, formal modelling within the contemporary cultural evolution literature has tended to idealise away key features of this consensus picture. Large families of models represent culture via a small number of traits, and, further, represent such traits as 'atomic' elements with no substantial interaction between them (e.g., Durham, 1991; Henrich, 2001; Kitcher, 2001; Henrich and Boyd, 2002; Rogers, 2010)—with a few notable exceptions (e.g., Enquist et al., 2011; Kolodny et al., 2015). Typically, when multiple traits are represented, they are taken to vary along a single dimension (e.g., Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Henrich, 2004), or function as an index of some other feature of interest (e.g., Fogarty and Creanza, 2017; Fogarty, 2018). While these models are all significant achievements, by idealising away multiple traits and trait interrelationships, they may be unable to represent a range of phenomena; notably those where the clustering of traits influences the downstream origination, distribution, and change in the trait pool over time.

Consider, as an illustration of the complex relationships among traits, communities of the Tyva Republic. The Tyva are pastoralists who engage in seasonal migrations. As they migrate from pasture to pasture, the Tyva engage in costly rituals around cairns that mark out pasture boundaries, regional borders, and salient geographical landmarks. These costly rituals involve offerings of food, tobacco, money, and the performance of ritualised behaviour. As experimental and ethnographic evidence shows, a plausible explanation for the origin and persistence of these costly rituals appeals to the Tyva's pastoral subsistence strategy. The rituals demonstrate to nearby populations the acknowledgement of local norms, and in so doing, may diffuse potential tensions about the use of common resources—such as pasture lands—by unfamiliar and potentially untrustworthy economic free riders. The costly rituals, then, signal trustworthiness and cooperation to the groups whose land may be being crossed and grazed (Sosis, 2005; Purzycki, 2010, 2011, 2016; Purzycki and Arakchaa, 2013).

This example shows how a rich system of interlocking religious practices, moral judgments, and patterns of subsistence can jointly explain the origin, organisation and persistence of costly rituals as a solution to intergroup relationships and the management of resources. Such a complex explanation, however, requires explicit consideration of multiple cultural traits, specific ecological circumstances, and salient interrelationships between the two.

The case of the Tyvan pastoralists is illustrative of the need for a broad theoretical and empirical endeavour aimed at capturing the dynamics of multiple cultural traits and their interrelationships. Here we motivate a *systems approach* as such an endeavour. We do so by examining implications of such an approach for key features of social transmission and the acquisition of traits, and how these generate macroevolutionary patterns and features. We illustrate these with simple models, and draw on a range of empirical and theoretical literatures to suggest how such models might be expanded into a broader research program. Though we here adopt a graph representation of trait interdependencies for modelling culture and cultural change, we nonetheless think there may be multiple ways of modelling cultural systems that better represent the complexity and heterogeneity of its constituent parts. Given this, the current paper may best be understood as offering one avenue through which a more fully-fleshed systems approach—that is, a distinctive approach encompassing novel models, concepts, and research questions—may be realised. The major contribution of this paper is to lay the conceptual foundation for such a research endeavour.

Despite the limited aspirations of the current piece, the conceptual ground-clearing we undertake here does suggest some immediate methodological and epistemological benefits that come with adopting a systems approach. Importantly, the explicit representation of traits and their interrelationships highlights how traits themselves function as a novel medium through which causes of cultural change can intersect at multiple levels. As we suggest below, the traits agents acquire can change how they learn, modulating the overall behaviour of the population in which they are a part. At the same time, the aggregate behaviour of the population can influence the availability and valence of such traits. The systems approach thus highlights how individual (micro) and population (macro) levels can influence one another through effects on trait relationships and availability. Here we predominantly focus on the first of these levels, looking at the effects of multiple traits and their interrelationships at the individual level. Yet we expect these models to complement the growing body of macro-level models (Kandler et al., 2012), and we return to consider multilevel causation and macro-level phenomena more fully in the discussion section.

A second important upshot is that a systems approach allows for the modelling of processes of path dependence and self-organisation (Enquist et al., 2011). Already well-recognised within evolutionary and systems biology (e.g., Kauffman, 1993, Carroll, 2005, Sansom, 2011), network interactions can impose structural and situational constraints that influence the synchronic behaviour and diachronic constitution of such networks. The graph-based models we adopt here provide some of the first links between this literature and cultural evolutionary theory—links that we also consider in more detail in the discussion.

The plan for the paper is as follows. After a brief introduction to the approach in the next section (§2 'What is a cultural system'), we highlight four domains of phenomena for which the systems approach has implications at both the microlevel and macrolevel: the cultural evolution of decision rules ('filters') and their influence on the distribution of cultural traits in a population (§3 'Cultural filters'); the contingency and stochasticity of system trajectories through a structured state space (§4 'Evolutionary trajectories and historical dependencies'), where trait interrelationships modulate rates of cultural change (§5 'Stability versus change'); and, where trait interrelationships contribute to inter-group differences in realised traits (§6 'Group phenomena'). We conclude by highlighting a number of possible avenues for future research, noting that a systems approach is poised to formalise and make explicit theories and hypotheses concerning culture that have been made in the humanities and social sciences.

What is a cultural system?

Researchers identify a wide variety of entities as candidate cultural traits. Typical lists include such diverse things as beliefs, myths, stories, and material artefacts, and often include larger societal structures like practices, norms, and institutions, like kinship systems or subsistence strategies (see e.g., Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Mesoudi, 2011; Henrich, 2016). Many of these elements bear connections, or relational properties, to one another that impact the acquisition, maintenance, and transmission of other traits. Beliefs, for instance, bear evidential and entailment relationships to other beliefs. If I believe that the dice are loaded, then I should change how often I expect to roll a seven. Material artefacts bear relationships to one another, often in ways that affect their functioning. Tin and copper, for instance, combine to make an alloy suitable for weapons and cookware, while tin and mercury make an amalgam suited for silvering mirrors. Speaking generally, models adopting a systems approach aim at capturing three key features: an explicit representation of multiple traits (perhaps of multiple trait types); trait relationships of different valence and character; and how traits and their relationships generate dynamic interactions over time. To put the motivation for a systems approach briefly, in human cultures, traits bear a wide range of relationships to one another, and these can have a variety of important consequences.

In the illustrations of this paper, we represent traits and their relationships as weighted graphs, where the nodes are the cultural traits, and there is a weighted edge with a positive value between two nodes if the traits are compatible, and with a negative value if they are incompatible. Relationships can also be asymmetric and represented with directed edges. In our simulations, there is a well-mixed population of agents, who are gradually replaced through a birth-death process. Agents can acquire traits either by inventing, through sampling from the universe of available traits, or by copying other agents. Agents copy traits with a probability proportional to how compatible the observed trait is to all other traits in the agent's current repertoire. The ideas in this paper are most clearly illustrated using small cultural systems and trait universes, so we will typically include only a few traits in the models, but our approach is general and could easily be scaled up to include many traits, with a range of asymmetric compatibilities on a continuous scale. For a specification of the simulation model and the parameter values used in the different examples, along with Python code implementing it, see the Supplementary information.

One important kind of consequence of a systems approach bears upon how traits may be distributed in a population. To see this, consider a simple model with four trait types: A, B, C, and D. Assume that these trait types begin with equal starting frequencies in a generational model with random copying. On the

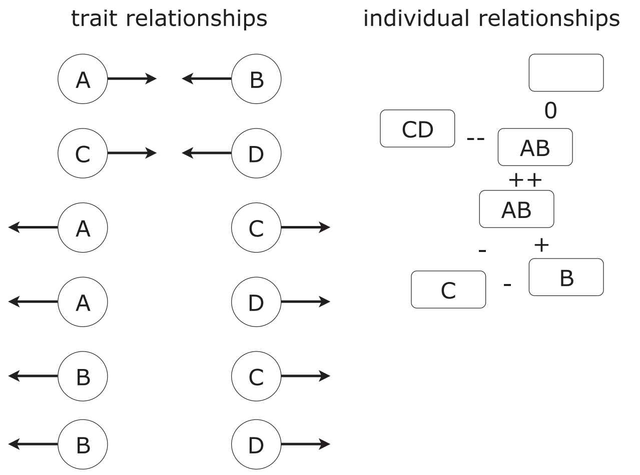

Fig. 1 Cultural system with simple attraction and repulsion. The left panel shows which pairs of traits attract and repel, and the right panel shows an example with individual repertoires and relationships between individuals

assumption that traits are acquired independently of one another, one would expect the frequency of trait types to be autocorrelated over time, varying only with the vagaries of random copying. Yet when pairwise relations are introduced—for instance, where traits pairs (A, B) and (C, D) (or AB and CD for short) facilitate the acquisition of their partners and inhibit the acquisition of other traits (e.g., C and D inhibit the acquisition both of A and of B, and vice versa) (Fig. 1)—this simple arrangement generates very different dynamics, ones that eventually settle into an equilibrium state where most agents have either AB or CD trait pairs (Fig. 2).

Of course, the nature and effects of trait interrelations themselves may change over time. This too is an important consequence of approaching culture as a system constituted by linked elements. Note that a preference (for a cultural trait) can also be considered a cultural trait. Shifts in preferences and beliefs are particularly noteworthy, as these both govern behaviour and change constantly in the face of exposure to new evidence and ideas (Fig. 3). In our modelling framework, preferences could be modelled with a positively weighted edge from the preference trait to the preferred trait.

The complex tangle of changing traits and relationships can be illustrated by looking to the work of Heidi Colleran and colleagues (2015; Colleran, 2016; Colleran and Snopkowski, 2018) on the demographic transition—the decline in fertility that has been observed in multiple human populations over the previous two centuries. The demographic transition is a striking trend, with families around the world increasingly limiting themselves to two or fewer children. It is also an unusual trend, evolutionarily speaking, since standard evolutionary reasoning would hold that organisms should produce as many viable offspring as their resources allow.

As Colleran articulates it, the demographic transition is a complex phenomenon, with tangled and imbricated causal processes interacting at multiple levels. Decisions on childrearing are influenced by the makeup of social networks, the prevailing social norms, ties among kin groups, socioeconomic classes, and more encompassing structures such as the regulations and institutions of the local polity and state. Nonetheless, distinct causal pathways and their effects can be discerned. For instance, combining ethnographic work with sophisticated network and statistical analyses, Colleran (2016) and Colleran and Mace (2015) were able to chart the distribution of contraceptive strategies used (if any) among a group of communities in Poland—separating out general contraceptive strategies (any decision or strategy for

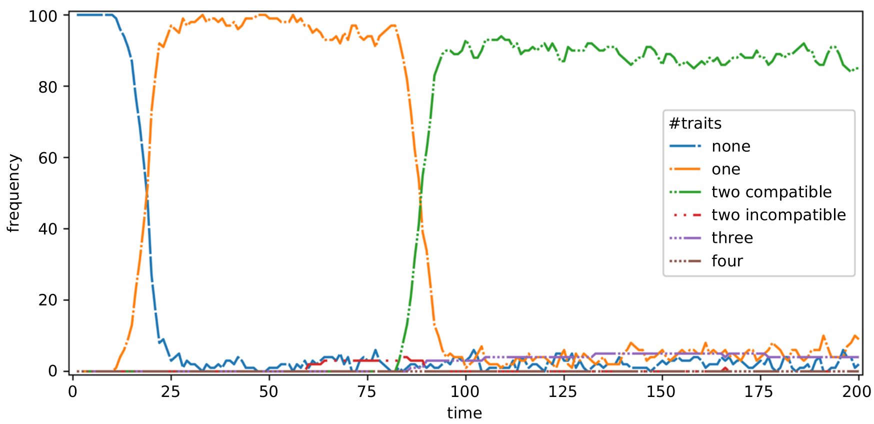

Fig. 2 Number of individuals with 0 to 4 traits, over time. Two traits can either be compatible or incompatible

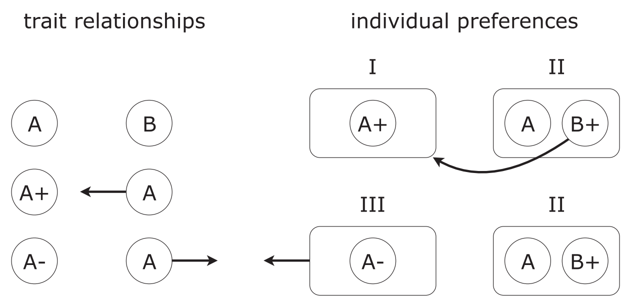

Fig. 3 Cultural system with preference traits. The left panel shows examples of traits relationships, where + indicates a preference for a trait, and - a preference against it. The right panel shows examples of three individual repertoires, where II acts as a cultural model. Individual I is more likely to copy II, including the preference for B, since I prefers A, while individual III has an aversion to II due to trait A

controlling fertility) from 'artificial' contraceptives (encompassing a range of modern contraceptive technologies).

Colleran's explanation highlights both individual-level and population-level causes. At the individual level, agents exerted variable influence: knowledge and use of contraception strategies by close kin and friends were key causal factors in determining not only whether any particular individual would use contraception, but also the particular strategy adopted. Yet community level indicators such as religiosity and education played an important role modulating and changing both the rate at which contraceptive strategies diffused through populations, and the particular strategies adopted. Highly educated populations accelerated the adoption of contraceptive strategies in general, but had limited effects on the spread of artificial contraceptives. Highly religious populations, on the other hand, tended to slow down the adoption of artificial contraceptive use, but not the diffusion of contraceptive strategies and decision-making more generally. Thus while individual networks and the transmission of knowledge and preferences are important, average population-level characteristics also influence the diffusion of contraceptive strategies by changing the background conditions against which individual transmission occurs (Colleran and Mace, 2015).

This example illustrates both the aspirations and the difficulties of a systems approach to culture: there is an enormous range of possible traits and trait relationships that are affected by wide-ranging causes. We cannot hope to offer an exhaustive taxonomy of such entities and effects in this paper. Nor do we suggest that the models we develop here provide more than thumbnail sketches as to how multiple interrelated traits might influence the composition and structure of culture over time. Nonetheless, by combining illustrations using graphs and simulation models with existing empirical research, we hope to articulate a number of implications of such models, sketch a number of compelling research objectives, and provide the conceptual tools for developing a distinctive systems approach to culture.

Importantly, we see the humanities and social sciences as playing an important role in the development of a systems approach. From Marxist approaches to postmodernism, researchers in philosophy, anthropology, literary studies, sociology, and many more besides have developed a range of theories and hypotheses about how best to describe cultural traits, their interrelationships, and the structures that they produce. It would be an overwhelming task to summarise the riches of the many fields in the humanities and social sciences, but we suggest that these resources have mostly not been integrated into the datasets or everyday theorising of cultural evolutionary research.

The reasons for this lack of integration may be a number of disciplinary and methodological features. One might be reticence on the parts of humanities and social scientific scholars regarding the past history of unilinear theory, which promulgated racist and Eurocentric accounts of cultural development and change (Steward, 1955). Another might be the failure of current work in cultural evolution to speak to the phenomena that interest researchers within the humanities and social sciences, perhaps because of mutual ignorance of the rich literatures within the humanities and social sciences (Ingold, 2007) and of cultural evolution (Lewens, 2015). Or, perhaps, the lack of integration may reflect methodological differences, with many of the theories and results of the humanities being resistant to formulation in formal, quantified models (Mesoudi, 2011).

These are all legitimate explanations for the lack of integration and conversation between the cultural evolutionary literature and other scholars within the humanities, social sciences, and natural sciences. Yet we think one roadblock not sufficiently addressed concerns the family of models used by many cultural evolutionary researchers. While humanities and social science scholars are interested in complex phenomena—often involving the interaction between behaviour rich in semantic information, networks of social interactions, material artefacts and persisting institutions—many prominent cultural evolutionary models focus on the evolution of a few select cultural traits, or traits that vary along a single dimension (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Durham, 1991; Mesoudi et al., 2006; Rogers, 2010). Moreover, when such models do build in more traits, these typically are taken to evolve independently of one another (Hahn and Bentley, 2003; Henrich, 2004; Bentley and Shennan, 2005; Enquist and Ghirlanda, 2007; Enquist et al., 2008; Strimling et al., 2009; Eriksson et al., 2010; Aoki et al., 2011). Though these families of models are impressive, and have generated a rich body of research, they represent a substantial epistemic gambit, one akin to that undertaken by mid-twentieth century work in population genetics (Provine, 1971). Within cultural evolutionary theory, this strategy holds that the dynamics and structure of cultural evolutionary phenomena can be extrapolated from models that represent a small number of cultural traits interacting in independent (or non-epistatic) processes. This kind of strategy licences the modelling of simple trait systems, either with an eye to describing the kinematics of those simple systems, or to illuminate the evolution and operation of mechanisms underpinning their transmission (e.g., Boyd and Richerson, 1985; Henrich, 2004).

To be clear, many, but by no means all, modelling families in contemporary cultural evolution are based on equations and results drawn from populations genetics. Yet, even those that do not tend to adopt the epistemic gambit of extrapolating from simple trait systems that model only a few, independent entities. These models have produced an exceptional range of compelling theoretical and empirical results. Yet what we are stressing here is that these models need to be complemented by those that explicitly represent how multiple traits and their interrelationships together affect the downstream distribution and structure of the cultural trait pool. In these circumstances, a systems approach that explicitly represents these elements and their relationships is needed. We turn to highlight these scenarios in the next four sections.

Cultural filters

A common view among many cultural evolutionary researchers is that the cognitive architecture implicated in cultural evolution is composed of special-purpose evolved cognitive mechanisms (Sperber, 1996; Sperber and Hirschfeld 2004, 2006; Boyd and Richerson, 2005; Richerson and Boyd, 2005; Mesoudi, 2011; Sperber and Mercier, 2017). As a case in point, early cultural evolutionary models (e.g., Boyd and Richerson, 1985) explicitly assumed that mechanisms for social learning and selective social learning strategies were under genetic control. Subsequent modelling and empirical work continued to assume the innate nature of these strategies—like prestige bias (Henrich and Gil-White, 2001) and conformity bias (Henrich, 2001)—usually on the basis of their perceived ubiquity in human populations (cf. Henrich, 2016).

Yet recent empirical research challenges many of these assumptions. Consider the recent work on selective social learning—the capacities involved in adopting particular strategies for learning from others. Work in both experimental and developmental psychology plausibly suggests that selective social learning strategies emerge from simple associative learning, where learners acquire links between certain individuals or cues and the value of information (reviewed by Heyes, 2018). This dovetails with developmental results that suggest that children preferentially attend to models on the basis of a number of cues, including competency, reliability, status, and certainty, as well as features including relative age, resemblance, and sex (Wood et al., 2013). Other evidence suggests that the nature of the cues, and their weighting in particular circumstances, is also controlled by associative mechanisms (Behrens et al., 2008; Heyes, 2018). Selective social learning may thus result from simple mechanisms of learning conjoined with exposure to the local structure of the informational landscape. Such exposure leads to the association between simple cues and the identification of agents bearing useful information across a range of situations.

More generally, there is growing empirical research supporting the claim that even central capacities of human social learning may be culturally evolved. Philosophers and psychologists have recently argued that the plasticity of human psychology provides opportunity for the acquisition not only of strategies for learning (as above) but also of novel cognitive functions. Kim Sterelny (2003), for instance, has argued that mindreading capabilities—the capacity to attribute and explain behaviour using mental state attributions—are assembled in development in an environment "soaked not just by behaviourally complex agents, but with agents interpreting one another" (p. 222). Such an assertion is backed up by a range of empirical results that suggest that the acquisition of key capacities differs in sequence and rate across different developmental and cultural circumstances (Siegal and Peterson, 2008; Wellman and Peterson, 2013; Shahaeian et al., 2013; Peterson et al., 2017). More recently, Cecilia Heyes (2018) has argued that not only mindreading, but also imitation, selective social learning strategies, and language may be the result of simple domain-general learning capacities occurring within culturally enriched, and perhaps designed, learning environments.

These accounts suggest that cultural evolution may be critically involved in the evolution of what we call *filters*: 'decision rules' that modulate the flow of traits in a cultural system.[2] These filters not only include those involved in *acquiring* traits—such as is the case with selective social learning, which sifts and sorts different sources of information—but also those involved in *innovating* (deciding whether to introduce a trait or set of traits to a system) and *diffusing* traits (deciding, out of many traits, which to express). We call these capacities 'filters' because they do just that: they filter out some traits while letting others through.

At this point, it is helpful to distinguish between *origin explanations* and *distribution explanations* (Godfrey-Smith, 2012). The accounts emphasised above provide origin explanations, which aim at explaining how a particular trait came about, often by pointing to studies in palaeoanthropology, developmental and experimental psychology, and cognitive neuroscience that lay out the evolutionary and developmental circumstances required for certain capacities to come about. Sterelny (2003) and Heyes (2018) are exemplary in this regard in bringing together a wealth of such data in their synthetic cultural evolutionary accounts of the origin of critical cognitive capacities of human beings.

Distribution explanations, by contrast, explain the distribution of traits in a population, or across populations. Food preferences represent one domain where filters may contribute to a distribution explanation. There is great between-culture variation in patterns of acceptance and rejection of food, and individuals are often strongly influenced by their cultural backgrounds in what foods they come to like or find distasteful (Rozin, 1988). Though only supported anecdotally, acceptance of fermented foods—for example, the slimy Japanese soybean ferment called *natto* or the strongly ammonia-scented fermented shark *kæstur hákarl* from Iceland—is often highly regionalised and culture specific (Katz, 2012). This may be because food acceptance or rejection is often tightly linked to culture-specific norms around what is considered disgusting (Rozin et al., 2016). Fermented foods are, after all, foods in a controlled process of decomposition. In this example, culture-specific norms influence individuals in filtering out possible traits (*natto, kæstur hákarl*) as incompatible with those they already possess.

In the discussion, we offer some speculations as to how a systems approach may contribute to origin explanations. But by and large, the graph operationalisation of cultural systems adopted here is apt for providing distribution explanations that demonstrate how cultural filters might modulate downstream distributions of traits.

We close this section by considering two ways in which such modulation might occur. The first is through *direct*, or *trait, filtering*, where the relationships between traits influence the distribution of other traits. The case of food preferences is case in point. Here, the history of trait sampling by a population means that only some traits are available for individuals to acquire. These realised traits then influence decision making: some foods are desirable, while others are filtered out in virtue of being disgusting.

Yet traits might also be modulated through *indirect filtering*, for instance, where such filters determine with whom one associates. One such indirect filter is the example of selective social learning (or model-based filtering) given above, where individuals selectively choose from whom to learn on the basis of informational cues. With such a filter, the traits one acquires will be skewed by the model one is oriented towards. Another indirect filter is a *similarity filter*, where individuals associate with others who bear similar traits (sometimes called *homophily*), either through deliberate choice of association, or by pruning their social networks of individuals with dissimilar traits (Axelrod, 1997; Centola et al., 2007). Unsurprisingly, similarity filters decrease the within-group heterogeneity while increasing the across-group heterogeneity of realised traits.

Evolutionary trajectories and historical dependencies

Interdependencies among traits reduce the number of sets of cultural combinations that are likely or even possible, and as a consequence, the number of likely or possible evolutionary trajectories that lead to those assemblages. For clarity of illustration, we will here consider strict dependencies, such that traits are not only facilitated by, but also contingent on, the existence of other traits. This can be illustrated by a simple unidirectional example. Consider ten traits, labelled by the first letters of the alphabet. Were the traits to be unilinearly dependent, as in Fig. 4a, subject to stepwise acquisition—such that B was contingent on the existence of A, C on B, and so on—then there are only ten possible cultural combinations: one for each trait, including all the preceding traits it is contingent on. There is also only one trajectory for each combination: the one that passes through each trait in alphabetical order, up to the last possible addition.

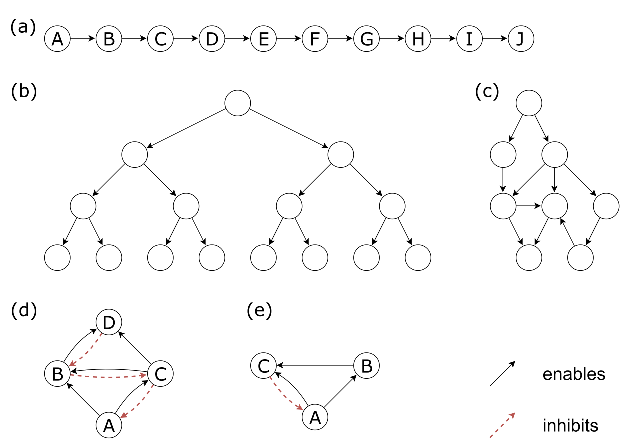

Fig. 4 Example dependencies between traits. Here, traits are (**a**) unilinearly dependent, (**b**) arranged in a tree structure, (**c**) combined in different ways. Traits can also be acquired in different sequences (**d**, **e**) and inhibit other traits

Compare this to the case where traits are independent, with no limitations on the order of acquisition. In this case, the state space of possible combinations explodes. Any combination of traits is possible, so the state space equals the power set of the ten cultural traits, meaning that the number of potential combinations is $2^{10} = 1024$ (minus one if we exclude the case of having no culture), and doubles for every trait added. The number of evolutionary trajectories that lead to such states is almost ten million ($\sum_{i=1}^{10}\prod_{j=1}^{10} j = 9,864,100$). Interdependencies thus provide a path dependence that can significantly facilitate the emergence of a particular cultural system on several occasions.

Relationships between traits can also lead to more complex and diverse cumulative culture, beyond the trivial accumulation of making culture larger by adding independent elements to a collection of traits, and beyond the predetermined stepwise acquisition of the previous example.

Cumulative culture is likely to be a significant contributor to path dependence in cultural evolution. When traits are preserved and build upon past innovations, culture generates *traditions*—historical chains of cultural variants linked through patterns of cultural transmission. Cultural evolutionary researchers often use the metaphor of a 'ratchet' to describe this historical process, since like a ratchet, things move steadily in a single direction—changes are kept, 'ratcheted', into the future rather than 'slipping back' over multiple transmission events (Tomasello, 1999; Dean et al., 2014). This ratcheting metaphor is meant to capture the way that cumulative culture differs from a range of possible (cultural) evolutionary scenarios—for instance, where evolution occurs stochastically, moves cyclically through a range of variants, or merely tracks environmental features in ways that do not involve building upon priorly held cultural variation. In so doing, cumulative culture can explain the production of climate appropriate clothing (Boyd and Richerson, 2005), counter-intuitive food extraction and processing techniques (Henrich, 2016), social organisation and institutions (Bowles and Gintis, 2013; Richerson et al., 2014), the differentiation and specialisation of tools (Basalla, 1988), and culturally evolved cognitive novelties (Heyes, 2018). Because cumulative culture produces traditions where future states of the tradition depend on the past states of that tradition, it is the kind of process that generates path dependence.

There have been only a few attempts within the cultural evolution literature that describe or model path dependence, partly since most previous models cannot describe historical processes of 'ratcheting' in ways that account for dependencies between traits. One recent exception is a model of the cumulative evolution of technology (Kolodny et al., 2015). Central to the model is a highly structured description of a cultural state space, which delimits three kinds of cultural innovations. The structure involves a central 'main-axis' with stepwise modification as in the unidirectional example above, but each trait on the main-axis can also be modified in a separate direction, to create 'toolkit innovations', and traits on the main-axis can be combined. While this sequential and combinatorial structure may be apt for understanding the evolution of (some aspects of) technological evolution, it seems less apt for characterising the opportunistic and creative processes involved in myth and storytelling (Morin, 2016; Acerbi et al., 2017), ritual and religions (Whitehouse, 2000), or social norms and institutions (Sperber, 1996; Bowles, 2004).

The combinatorial combination of traits in Kolodny and colleagues' model draws attention to the various relationships between traits. As illustrated by Enquist et al. (2011), two important kinds of interdependencies that can structure the cultural state space includes the combination and differentiation of elements. A sweater consists of a combination of cloth and thread, items which can be used also for other purposes. Even though a needle is not part of a sweater, it vastly facilitates the creation of one. With the further introduction of cultural traits, for example, dyes or pigments, we can have a differentiation of sweaters, such as different colours. Simple graphs exemplifying such relationships are given in Fig. 4b, c. Representing relationships between traits in graphs like these enable us to easily describe facilitative and inhibitory relations, characterise the possible and likely trajectories of cultural evolution, and to consider how such relationships among traits themselves might produce new kinds of path dependent phenomena.

The existence of an organised—that is, structured—cumulative culture means that culture can carry traces of its historical trajectory, and, thus, has *deep history* (Sterelny, 2014; Sterelny and Hiscock, 2014). To illustrate this, consider the graph in Fig. 4d, with four traits, A, B, C and D, of which the latter three depend on the existence of another trait, and which can all be inhibited by another trait. For clarity of illustration, let us assume that the inhibition is strong enough to completely suppress the inhibited trait, such that the carrier loses it.[3] Were these traits to be independent, there would exist $2^4 = 16$ possible cultural states (including the possibility of having no culture). The traits of such independent assemblages may have occurred in any order (and if traits can disappear and reappear, then potential evolutionary trajectories are boundless), and as a result, the state of a particular system contains no information on its history, except that its constituent elements must all have occurred (at least once) at some point. The relationships between traits, posited in Fig. 4d, halves the number of possible states, and there is one unique trajectory leading to each of these states. The possible states that include at least one trait (and the corresponding trajectories) are: {A} (A), {B} (A → C → B), {C} (A → C), {D} (A → C → B → D), {A, B} (A → B), {A, D} (A → B → D), and {C, D} (A → C → D). Even if the present state of a cultural system does not include all traits that had (at some point) been acquired over their evolutionary trajectory, the scheme of relations makes it possible to recreate their evolutionary history. The fact that culture, due to these structural constraints, often carries so much of its history also enables cultural evolution to have complex path dependence while having the Markov property in terms of predictability: while historical events dictate where we are now, the future cultural states depend only on the present state.

It is a straightforward conclusion from the fact that cultural traits can have downstream effects arising from their interrelations, or compatibility, that acquiring certain traits can have vast effects on which traits can be acquired later on, and thus potentially lead to cultural systems that differ in most of the traits they include. For an extreme example, consider the tree-like structure in Fig. 4c. Each new acquired trait prevents the acquisition of the traits on the other branch, by making them unreachable.

Yet it is not only *which* traits are acquired that determines which cultural states are accessible, but also the *sequences* of events can determine which traits can coexist. Let the traits B and C be dependent on A, and B be compatible with C but inhibit A, as in Fig. 4e. The two traits B and C can then be maintained simultaneously, in the same system, provided that B is acquired first. If, on the contrary, C is acquired first, then there are no traits allowing for the acquisition of B. As an example, A may be a generic or non-explanatory answer to a politically charged issue, B a populist answer, and C a complex answer providing a real explanation. B could then be attractive enough not to be lost in a population even in face of a real answer, and even if it would not appear if there already existed such an answer, while C could easily replace the unsatisfactory answer A. The importance of the sequence of acquisition is further amplified if B and C enable different clusters of traits down the line.

For a more concrete example based on Fig. 4e, consider the Lancet MMR autism fraud. In 1998, former physician Andrew Wakefield (A) submitted a paper linking the MMR vaccine to colitis and autism spectrum disorders. (B) The paper was accepted and led to a drop in vaccination rates and a loss of confidence in their safety, with a concomitant increase in anti-vaccination propaganda (e.g., Gross, 2009). However, the paper was filled with flaws, the results had been misinterpreted, it had been conducted unethically, and its main findings were later refuted, which led to (C) a late rejection (a retraction) of the paper by the Lancet twelve years later (Dyer, 2010). Even so, the strengthening of the anti-vaccination movement that B sparked, and the spread of anti-vaccination ideas it caused, was not cancelled out by C. Had the paper been rejected, C, directly, without publication, then that would have inhibited B and its consequences.

Stability versus change

Empirical observations of cultural phenomena reveal extensive variation in the rate at which culture changes. These rates can range from traits and systems that remain more or less the same over many generations, to traits and systems that change rapidly within a single generation. For instance, there are many examples of religious beliefs and social norms that have remained similar over long periods of time (Geertz, 1973; Glenn, 2010). At the same time, however, clothing styles may be subject to fast changes (Shepard, 1972; Belleau, 1987, Herzog et al., 2004). Not only are there diverse rates of change, but these rates themselves may also change over time. To give one example, Gjesfjeld and colleagues (2016) show how changing rates of origination and extinction rates have changed the landscape of car models, with competition between manufacturers being a substantial driver of a decreased diversification in automobile models. And, of course, different elements within culture may vary in their rates of change. Comparative and phylogenetic studies of language evolution, for instance, demonstrate both fast and slow changes in different lexical and grammatical elements (e.g., Greenhill et al., 2017).

A number of explanations have been suggested for the variation in the rate of change in cultural evolution, including external factors such as the physical and ecological environment (Vegvari and Foley, 2014), demographic factors (Powell et al., 2009), and cultural complexity (Querbes et al., 2014). Here, we explore how trait relationships and a systems view of culture could potentially explain variation in the pace of cultural change. Two factors seem important to consider. One is the intrinsic properties of traits that determine their relationships with other traits, and the other is filtering processes that may favour collections of traits that either promote stability or drive change. We first consider trait relationships that can promote stability and then relationships that can drive changes. We end with describing systems with fashions or fad-like dynamics, in which traits may change more quickly than when they are modelled as independent traits.

It is a plausible extension of the idea that traits are more or less compatible with one another that traits which mutually support each other's transmission could form stable cultural clusters that are maintained over many generations. We have investigated this idea in a series of simulations similar to those in the other sections. Here we generated a situation with 20 traits with predominantly negative relationships, and explored how groups of two, three or four mutually supporting traits could influence each other's existence in such a trait environment. Examples of these simulations are illustrated in Fig. 5 (see the Supplementary information for more details). It shows, in the situation explored, that two mutually supporting traits promote each other only ephemerally, with three traits the effect was stronger, and finally

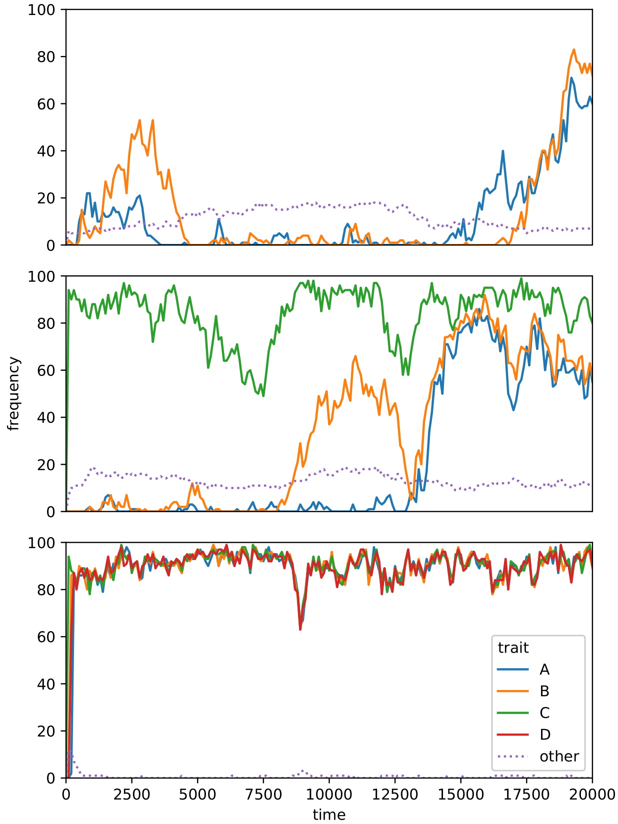

Fig. 5 Mutual support may maintain system configurations over a long time (where a time step is one round of interactions). The number of traits supporting each other is two in the top panel, three in the middle panel and four in the bottom panel, from a total of twenty traits. The figure shows the frequencies of the supporting traits and the average frequency of the other traits included in the simulations

with four traits a stable cluster was formed. Note that two traits have only one relationship; three traits have three relationships; and four traits have six relationships that can support stability (in general, $n(n-1)/2$, where n is the number of supporting traits).

Though the model emphasises the stability brought about through compatibilities between traits, incompatibilities or negative relationships could also contribute to a stable cluster if these inhibit traits outside the present cluster. This would decrease the likelihood of new traits invading the cluster in question.

This supports previous work showing that such conservative tendencies can easily evolve (Ghirlanda et al., 2006; Acerbi et al., 2009; Acerbi et al., 2014). In these models, individuals are born open and acquire traits in interactions with other individuals. Whether copying occurs depends on how compatible the observed trait is with the other traits already acquired by the individual (this is what we call *trait* filtering above). The reason why conservatism evolves in these models is that open individuals are more likely to acquire traits that make them more conservative while conservative individuals are less likely to acquire traits that make them more open. Over generations, increasingly conservative systems become established.

As one can see, the stability of cultural systems—or as is more likely to be the case, specific trait assemblages—is plausibly promoted both by mutual relationships among its parts, and potentially by incompatible relationships with traits not part of the system. This describes one kind of evolutionary history; here, trait assemblages successively increase internal compatibility and decrease external compatibility. If such features were to characterise most traits of a cultural system, then one would expect such a system to eventually enter a basin of attraction where little subsequent change could occur. However, as we will see, there are also circumstances and arrangements of trait relationships that promote change.

While mutual support can give rise to stable cultural systems, there are other relationship distributions that will promote change rather than stability. Some arrangements may even give rise to rates of change that are higher than for independently evolving traits. One type of trait relationship that would promote change rather than stability is an asymmetric relationship between two traits: for instance, trait A may facilitate the acquisition of a trait B while B has the opposite effect on A (inhibiting its acquisition). Such an asymmetric relationship could lead to a succession of trait replacement events. If A appears first, then it will promote B, but when B becomes common, it will cause A to disappear. The processes are directly dependent on properties of the current cultural system and can lead to an accelerating generation of new cultural traits (Lehman, 1947; Ogburn, 1950; Enquist et al., 2011; Kolodny et al., 2015).

Theoretical work also shows how fluctuations in the rate of change may arise, with periods of rapid change interspersed with periods of slow change (Aoki, 2015). Within the humanities, a classical model for such fluctuations in the rate of change is the ideas of dialectic processes (Cohen, 1978), which recognises that cultural systems may give rise to internal contradictions that promote substantial changes to the system. This idea seems fully compatible with the theory of cultural systems suggested in this paper. However, we are not aware of any theoretical work demonstrating for instance a correlation between the rate of change and the degree of internal conflict or incompatibility in a system.

Evolving traits relationships may, under certain assumptions, give rise to very high rates of change typical of fashion or fashion-like phenomena (Acerbi et al., 2012, Michaud, 2019). To see this, suppose that there are two kinds of traits, both of which can be transmitted between individuals. The first kind is composed of display traits like a colour or a style, and the other preference traits, which are linked to specific display traits. During their lifetime, individuals acquire and display traits and preferences through their interactions with other individuals. This set-up has two consequences for the individual. First, the acquisition of display traits will increase or modify the individual's efficacy as a cultural model. If an individual's display traits are popular, then that individual will be copied more frequently than an individual with less popular display traits. Second, preferences acquired by the individual determines which individuals it will tend to learn from. Note that with these assumptions, there are no absolute or permanent standards for what makes a display trait popular.

Among a group of individuals, these social learning processes will give rise to a highly unstable but clearly patterned scenario of cultural evolution, in which systems of preferences and display traits change quickly in cycles of outburst and decay (Acerbi et al., 2012). A cycle starts with a preference for a particular display trait stochastically becoming common among currently popular individuals. This increases the spread of the preference in the population, which in turn spreads the trait. However, as soon as the trait starts to be common, the preference starts to disappear. The reason for this is that individuals with the preference change faster than individuals without the preference (see the discussion about evolution of conservatism above). Thus, more individuals with the preference will lose it than individuals without the preference will gain it. An example from the model of Acerbi and colleagues is shown in Fig. 6 with the lag between preference and the corresponding display trait. The changes that occur in this

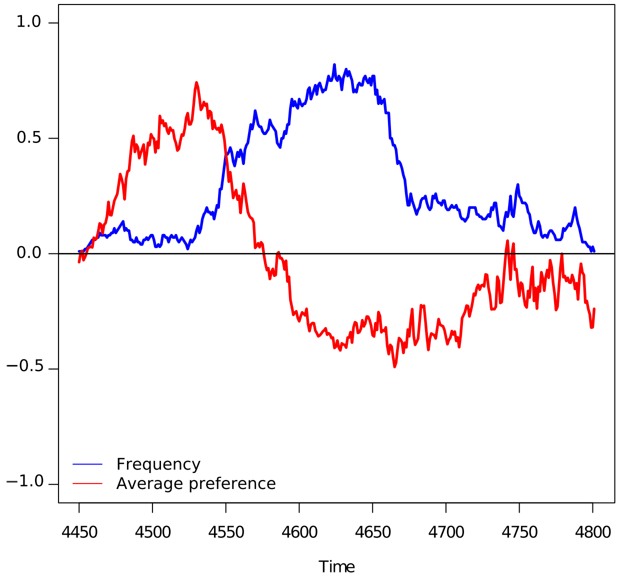

Fig. 6 Example of a fashion cycle generated by an evolving mixture of display and preference traits. The example is based on the model of Acerbi et al. (2012)

model can be faster than the rate of change occurring when traits evolve independently of each other, because both the rise and fall of the display trait are actively driven by the fast changes in preferences.

In most examples in this paper, trait relationships are assumed to be fixed and exogenously given, for instance by the nature of traits, logical constraints, interaction with reality or genetic predispositions. However, in the simulation model of Fig. 6, the relationships between traits themselves are subject to cultural evolution.

Group phenomena

Cultural systems may also help to explain the emergence of cultural groups. A single trait may suffice to distinguish between members of different groups. Yet for the existence of such group-defining traits to be a causal factor influencing the behaviour of others—for instance, to serve as a signal for intra-group and inter-group biases or for overt prejudice towards other groups—and for the existence of the trait to be formed and maintained, such a trait needs to be interdependent with those that induce the relevant behaviour.

There are numerous examples of how important groups are for dispersal of ideas about the world and our behaviours towards other people, and how easily they form. A famous example is the minimal group paradigm (Tajfel, 1970; Tajfel et al., 1971), where discrimination emerges between groups based on arbitrary divisions. There is a vast empirical literature on group phenomena that we cannot cover here, but there are for example metastudies on group biases across cultures (Balliet et al., 2014; Romano et al., 2017), and surveys on how opinions and beliefs are reinforced in groups, polarising views on the societal level (Lamm and Myers, 1978; Isenberg, 1986; Abrams and Hogg, 1990) and on the importance of sharing several cultural traits for emotional closeness between individuals (Curry and Dunbar, 2013), showing that a cultural systems approach to understanding group formation may be viable.

Small systems of two or a few more traits may explain the maintenance of pre-existing groups in specific situations. In the modelling literature, there is typically an underlying strategic situation in the specified form of a game, usually a prisoners' dilemma, where the group structure supposedly facilitates altruistic behaviour by coupling the trait of a group marker with cooperative behaviour towards individuals with that marker. The objective of such studies is to find a mechanism for an ingroup bias. Typically such models are based on a biologically inherited marker (e.g., Riolo et al., 2001; Hammond and Axelrod, 2006; Jansen and van Baalen, 2006) that also requires spatial assortment and kin selection (see Read, 2010; Jansson, 2013) or rapidly changing markers (Fu et al., 2012). Changing the underlying game can replace the spatial assortment (Jansson, 2015) and also allow for cultural nonstatic markers to coevolve with behaviour (McElreath et al., 2003; Efferson et al., 2008). Typically, the models are based on strategic situations and try to explain cooperative behaviour exclusively to members of your group through some kind of greenbeard effect (Dawkins, 1976, 1982), group selection (Choi and Bowles, 2007), direct reciprocity through spatial structure or making group traits more flexible than behavioural traits, or reputation (Masuda and Ohtsuki, 2007; Grey et al., 2014) (for a review, see Masuda and Fu, 2015). As will be illustrated below, a cultural systems approach may contrast with such approaches by moving beyond strategic situations, pre-existing groups and biological inheritance.

There are also models implicitly based on simple cultural systems. Examples include polarisation and clustering based on shared traits (Schelling, 1971; Axelrod, 1997), set structured populations (Tarnita et al., 2009), and individuals structuring into groups (Grey et al., 2014). Schelling's (1971) segregation model, for instance, entails simple systems that can maintain homogeneous views among actors, or opposing views that are somewhat balanced in numbers of advocates. The latter systems are unstable, and the population ends up segregating into cliques of homogenous sub-populations. Similar patterns emerge when agents copy more from the agents in the vicinity with whom they already have the most in common (Axelrod, 1997). This idea is a bit more generalised and explicitly connected to cultural systems in what is referred to as evolutionary set theory (Tarnita et al., 2009). Here, agents can become and stop being members of any number of available sets, that is, they have a number of cultural traits, and they interact more with agents with whom they share many traits, again in a strategic situation facilitating cooperation between similar agents. An even more bottom-up approach to group formation is one where the ideas are about the other agents, and agents interact more when they gain positive experience from previous interactions, and where they also exchange views on third parties, leading to clustering (Grey et al., 2014). Apart from cooperative interactions, there are also models of how social network structure emerges from similarity in several cultural traits (Centola et al., 2007; Centola, 2015).

Using the framework of cultural systems suggested here, we can potentially generalise mechanisms of group formation, polarisation and prejudice further, as by-products of relationships between the traits that agents possess.

Consider the previous example of a cultural system with simple attraction between traits A and B, and C and D, and repulsion between all other pairs (Fig. 1). We saw that the cultural evolution of such a system leads to a dominance of compatible traits. Looking at the prevalence of the individual traits over time (Fig. 7), we see that, typically, the population has not converged on sharing the same pair of compatible traits, but the two systems, AB and CD, tend to coexist (for further details on the simulation, see the Supplementary information). The relationships between traits have thus led to the spontaneous formation of two incompatible cultural groups.

Contrasting with the previous modelling approaches described above, there are no utilities involved. Groups have not been

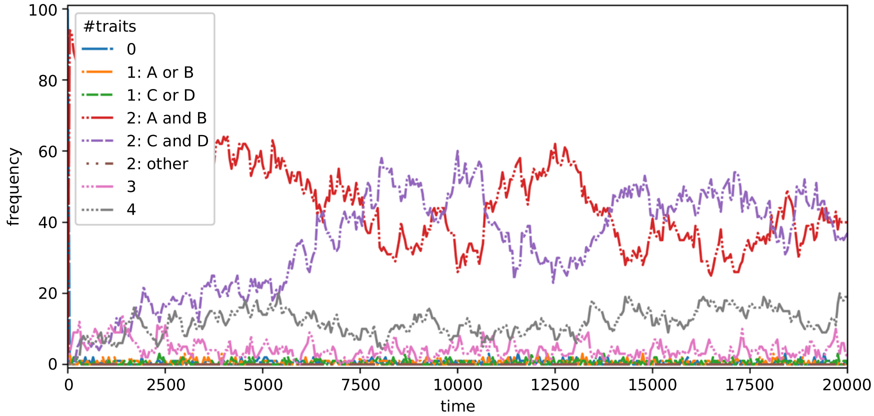

Fig. 7 Prevalence of cultural systems over time. Most agents have either traits A and B, or C and D

formed because it is rational or there is a selective pressure on the individuals, nor of spatial or social assortment, and the groups are defined only by cultural traits. This illustration merely points at the potential of explaining various group phenomena, and this particular example pertains more to polarisation into two camps than ethnic groups. However, with more clusters of mutually compatible traits, the population could polarise into several, and potentially overlapping, groups.

Relationships can also vary and be endogenous. A recent and related model specifically representing preferences (Goldberg and Stein, 2018) finds cultural variation divided into two clusters also when the compatibility between traits evolves culturally, through associative diffusion that takes place by pairwise displays and observations of cultural traits. When agents see two traits used together, they increase their association between them and make their preferences for them more similar, resulting in a cluster of traits that a part of the population likes and another cluster that they dislike, with the other part of the population having opposite preferences.

These cultural systems also provide opportunities for path dependence at the group level. New traits that enter the population might be absorbed by individual members of only one of the groups, depending on how they relate to existing traits, or even more groups may form. When clusters of compatible traits grow, the groups that are defined by them become more stable, and limit exchange between groups. Trait dependencies should thus not only allow for groups to form, but also for them to be maintained over time, and eventually be associated with beliefs, as well as behavioural and phenotypic traits. Examples may include prejudice, group biases and closeness between individuals.

At a more abstract level, this illustrates how multiple cultural systems can exist in parallel, also when the relationships between the traits are exogenously given (e.g., set by physical reality or logical constraints) and the potentially available traits are the same for all individuals in the population. At a higher-order level, cultural systems may themselves regulate the relationships between traits (e.g., having A and B may regulate how compatible C and D are). Cultural evolution may thus also give rise to multiple cultural systems that differ not only in what traits are included in a cluster, but also in how compatible those traits and potential traits outside that cluster are.

Discussion

The cultural systems approach articulated here highlights a range of novel and emerging research areas in the cultural evolutionary literature. We have here focused on its implications for four such areas: (i) the cultural evolution of 'filters' that modulate processes involved in acquisition, invention, and transmission; (ii) the path dependent trajectories of cultural systems that carry signals of that system's history; (iii) the rates of cultural change and diversification; and (iv) the formation and dynamics of cultural groups.

A noteworthy feature of these domains is that they display self-organisation: that the relationships between traits play a large part in which trait combinations are realised (in individuals, groups), and that these may, in turn, influence the downstream acquisition, innovation, and diffusion of traits. So, for instance, filters may themselves be culturally evolved decision rules aimed at optimising various goals, and path dependent explorations of trait pools may depend on the relationships holding between traits.

The modulating effects of self-organisation can be ephemeral, systematic, and everything in between—with the effect and duration of self-organised features contingent upon the vagaries of cultural evolution. Above we focused on the possibility of systematic influences, where cultural evolution itself provides the circumstances for the reliable acquisition of trait complexes and their effects in populations. This is for the simple reason that such complexes are likely to have pervasive and long-term effects, with broad implications.

The phenomenon of self-organisation is underappreciated in the modelling work of cultural evolutionary theory—even if the idea itself has some currency in the broader anthropological, philosophical, and evolutionary literature (e.g., Kauffman, 1993; Deacon, 1997; Sterelny, 2012). This may be because self-organising structures are only visible in approaches that represent multiple traits and their interrelationships. As we hope to have shown above, even when a few traits are employed, trait relationships can generate a wide range of interesting and novel dynamics. A cultural systems approach thus not only makes conspicuous self-organising phenomena, but provides a flexible set of tools for investigating and understanding them.

Another important feature of the systems approach is that it can address questions at multiple levels. We have here illustrated how cultural systems identify distinctive features at the trait, individual, and population level. As illustrated in Figs 5–7, the consideration of relationships between traits can enrich the dynamics of population-level outcomes through microlevel models. We also saw how such relationships could channel the characteristics of individuals, modulate homogeneity and heterogeneity, and alter the pace of cultural change. Such processes might also bring about group formation in stable clusters or fashion cycles, and can explain aggregate measures at the group level that are difficult to generate with independent traits.

To take one example, when discussing rates of change in fashions or fads, we highlighted how the acquisition of preference and preferred display traits can generate rapidly fluctuating dynamics at the aggregate level. A cultural systems approach can thus complement already existing strategies at employing 'population thinking' (Lewens, 2015) by exploring how the endogenous links within cultural systems interact with individuals to realise population-level phenomena. Mapping the link between microlevel mechanisms and macrolevel outcomes to the scheme of Coleman (1986), cultural systems along with frequencies of traits in the population pose structural and situational constraints on agents, who adopt traits selectively through copying and filtering, producing updated frequencies and a new subset of associated structural and situational constraints.

Thus, a systems approach provides a framework for understanding how individual actions generate macroevolutionary causes, and how these can feed back to influence microevolutionary interactions, via their influence on trait availability and interrelationships (such as preferences). Our models have focused predominantly on the first of these mechanisms, pointing to areas where a systems approach can illuminate how individual-level behaviour generates population-level patterns. For instance, trait interrelationships can drive differentiation between cultural groups and modulate the tempo and mode of cultural evolution. We have further suggested that cultural filters may be an important mechanism at play to change macroevolutionary patterns by influencing and modifying these trait interrelationships.

At the same time, we pointed to empirical work showing how population-level causes can influence individual-level behaviour by modulating trait availability and desirability. Heidi Colleran's work on the diffusion of contraceptive technology demonstrates how the influence of the average behaviour of the population (here, religiosity and education) can influence the availability and attitudes towards contraceptive knowledge and use. Group dynamics too can polarise and cause clustering of traits among distinct populations, further altering trait availability and desirability.

It is also possible that systems themselves may interact at the macro-level. Though we have not focused on such a possibility in this paper, we above highlighted the work of Erik Gjesfjeld and colleagues (2016) who explored the changing rates of origination and extinction in the production of car models. The system-level properties that feed into such origination and extinction rates—broad relationships between manufacturing strategies, state policies, demand cycles, oil production, and the like—provide yet another avenue of potential investigation for the systems approach.

As we hope to have stressed above, the idea of cultural systems is not a new one. It is not only a consensus view, but one that has long been subject to analysis and theorising in anthropological thought, especially where a range of thinkers have described cultures as systems subject to evolutionary change (Steward, 1955; Sahlins, 1960; Kroeber and Parsons, 1958; Geertz, 1973; Diener, 1980; for a general review, see Carneiro, 2003). Yet for the most part, these researchers deployed systems thinking in a qualitative way—often drawing a variety of analogies between cultures and specific systems like organisms or species. What is distinct about the approach motivated here—and what it adds to the already existing use of systems thinking—is that it employs the tools of formal modelling. The bottom-up style of systems modelling used in our examples is flexible and open-ended, providing the opportunity to explore a wide range of hypotheses by creatively modifying and combining different combinations of trait universes and agent properties.

This approach complements and generalises some recent models that have also adopted a strategy of modelling multiple traits and their interrelationships. Goldberg and Stein (2018), for instance, employ a similar framework to explore the role of what they call 'constraint satisfaction' in changing the trait interrelationships in a small trait pool (what they call a 'semantic network'). This work explores how the compatibility and incompatibility of traits can be socially constructed and modified over time. In a different vein, Claidière and colleagues (2014) employ 'evolutionary causal matrices' to explore the effect that trait types have on the absolute number of said trait types over time. This is mostly analogous to what we have discussed as selective trait filters. Without explicitly representing the compatibility or incompatibility between traits, or the specific decision rules that determine the acquisition or modification of traits, these matrices directly model the filtering effects that traits have on the downstream composition of both individual and group systems.

Speaking generally, we have here illustrated how a systems approach—particularly one that builds upon the strategy of investigating the strategies of acquiring, innovating, and diffusing culture in a rich trait universe—generates new tools for explaining cultural evolutionary phenomena. Already, the results given above reveal multiple areas for future enquiry. In particular, exploration that goes beyond disjunctive compatibility or incompatibility has the potential to generate a richer set of dynamics. At the same time, building in different kinds of trait relationships—such as those necessitating the sequential acquisition of certain traits—offers the possibility of exploring more realistic trait universes.

As we have suggested in numerous places above, a systems approach also has the potential to connect with, and help to explore, other issues in cultural evolutionary theory. In particular, it seems apt for exploring issues at the intersection of demography, population size, and the size of population-level cultural systems (Henrich, 2004; Powell et al., 2009. Cf. Vaesen et al., 2016). Along the same lines, it seems apt for connecting with the palaeoanthropological literature on the rates of change in cultural traits over time, where this includes both stasis and rapid change. The radical stasis of lithic technologies in the lower and middle Pleistocene and the radical change in culture that occurs in the Holocene (Mithen, 2005. Cf. McBrearty and Brooks, 2000) provide a rich set of phenomena for exploration by a systems approach.

As we noted above, many of the extant cultural evolutionary models are based on those developed in evolutionary biology. Researchers in cultural evolution motivate the adoption of such models by means of analogy: the seeming similarity of transmission processes in cultural and genetic evolution has given warrant for the exploration of cultural evolutionary dynamics based on models using replicator dynamics or other population-genetic tools. We do not here wish to contribute to the growing literature that explores how researchers have developed analogy (e.g., Sperber, 1996; Lewens, 2015). Instead, we merely wish to point out that analogies often function to highlight salient avenues of empirical research, and that there are many such fruitful avenues.

We have here been inspired in part by work in systems biology—particularly that which describes the evolution of organisation and constraint within complex dynamic systems (Kauffman, 1993). To illustrate this analogy, consider HOX genes—an important class of deeply conserved homeobox genes that regulate patterns of development across almost all eukaryotes (Bürglin and Affolter, 2016). HOX genes regulate the site-specific development of morphology, so that limbs grow in species-typical fashion (Krumlauf, 1994), and manipulation of these genes can lead to odd mutations, such as *Drosophila* with legs where antennae normally form (Carroll, 2005). HOX genes are one instance of a structure that, once it has arisen, persists over time—forming a set of tools that can be tweaked to generate diversity. They serve as a signal and explanation for the similarity in body plan across different evolutionary groups.

Systems biology studies such homeobox genes as an instance of 'constraint-based generality' (Green, 2015)—here understood as the ways in which systems tend to self-assemble a structure that constrains the possibilities in which it can change in the future (O'Malley, 2012). Some of these structural constraints that researchers have identified include core components and weak regulatory linkage (Kirschner and Gerhart, 2006), generative entrenchment (Wimsatt, 2001), and network robustness (Jaeger et al., 2015). These are structures that limit the evolutionary trajectories likely to occur, but in so doing, minimise the risk of lethal mutations, and, perhaps, increase the tempo of evolution.

Our guiding thought is that similar kinds of constraint-based principles and self-assembling features can help in understanding cultural systems. Like HOX genes, it seems likely that at least some cultural traditions are tightly integrated in virtue of their role in ensuring the socioeconomic viability of cultures over time (cf. Boyd et al., 1997). We expect these 'cultural cores' (Steward, 1955) to share several features, given their role in mitigating recurrent socioecological problems concerning resource allocation, free-rider problems, warfare, and the like (Sterelny, 2012, 2016). Such cores could be usefully explored using a constraint-based approach that investigates the likely trajectories that populations will traverse over evolutionary time frames.

Yet here we also urge caution. Along with other researchers (e.g., Richerson and Boyd, 2005; Mesoudi, 2011), we would stress that cultural evolution works differently from biological evolution. As has often been noted, the social nature of culture means that ideas, traditions, beliefs, and technologies can readily diffuse between populations. The free-flowing transmissibility of culture—though analogous to a limited extent with horizontal gene transfer—is likely to generate unique dynamics and rates of change. Cultural traits are not necessarily transmitted as one package, but are acquired and lost in multiple steps, with the consequence that they can be individually selected on how compatible they are to other acquired traits. This suggests that realised cultural traits in a population may have radically different histories and transmission dynamics.

Beyond developing new analogies to on-going empirical research, a systems approach to culture has the potential to connect with the wide range of humanities and social science literature that have made general hypotheses about the formation, nature, and dynamics of cultural change. As we suggested above, the idea that culture can be understood as a system has been a mainstay of anthropological thinking in the twentieth century. Yet these ideas are also found in the classical works of sociology, linguistics, and economics (Marx, 1867/1990, Saussure, 1959, Durkheim, 1995), and are now widespread throughout the humanities and social sciences. To touch on just a few areas, systems thinking seems to be implicated in understanding gender structures (e.g., Walby, 1989), social norms, attitudes and ideology (e.g., Boutyline and Vaisey, 2017; Inglehart, 2018; Jansson et al., 2013; Strimling et al., 2019), and systems of language (e.g., Greenhill et al., 2017), technology (e.g., Franklin, 1999), economy (e.g., Wallerstein, 1974), and religion (e.g., Geertz, 1973). A systems approach provides a promising bridge to the as of yet unexplored wealth of theorising about culture coming from within the humanities and social sciences.

Of course, a systems approach brings with it a distinct set of challenges. Compared to population-level models of single or independent traits, incorporating relationships between traits introduces a higher level of complexity. This decreases the tractability of cultural evolution models, while simultaneously increasing degrees of freedom. Given the wide variety of possible outcomes, modifying parameters might induce significant changes to modelling results.

It is uncontroversial that culture is an organised system. What we have argued here is that explanations of several cultural phenomena are sensitive to the relationships between traits, and, further, that empirical and theoretical research suggests that these phenomena are central to culture and cultural change. In other words, acknowledging trait interrelationships opens up rich dynamics that can generate empirically observable patterns unattainable for models that represent traits in isolation. This suggests that we should not shy away from the challenge of adding this extra layer of complexity to our cultural evolutionary models.

Simulation model

In the simulations, there is a universe of cultural traits with relationships between them. A relationship between two traits consists of a compatibility score of 1 if the traits are compatible, and −1 if they are incompatible. A universe is specified for each illustration in the manuscript (see below). There are 100 agents, each with an individual cultural repertoire, consisting of a subset of traits from the universe. At the outset, the agents are naive, with empty repertoires, but acquire traits through innovation (of traits from the universe) and copying from other agents.

The agents meet in random interactions. One round of interactions, or a time step, includes copying, invention and a birth death process. First, each agent, the receiver, samples one other agent as a cultural model. The model randomly selects one of the traits, i, in its repertoire for display to the receiver. The receiver copies the trait with a probability determined by the average compatibility score s of the trait with the receiver's current repertoire, that is,

$$s = \frac{1}{|R|}\sum_{j\in R} c_{ij}$$

where c_{ij} is the compatibility between i and j, and $R \neq \emptyset$ is the set of traits in the receiver's repertoire. If the receiver has no traits, $R = \emptyset$, then $s := 0$. The probability of copying is determined by the logistic equation

$$p(s) = \frac{1}{1 + e^{-10s}}$$

The constant 10 was arbitrarily chosen, but values below around 5 give the score a small influence and the results were not sensitive to scores above that value.

Each agent then invents a new trait with probability 0.001; that is, it randomly selects a trait from the universe and adds it to its repertoire (if the agent does not already possess the trait). Finally, each agent dies with probability 0.01 (0.0025 in Section 6 – the lower rate provides more stability), and is replaced by a new naive agent.

In the sections 'What is a cultural system?' and 'Group phenomena', the universe consists of four traits, A, B, C and D, where A and B are mutually compatible, and C and D are also mutually compatible, but all other pairs of traits are mutually incompatible.

In the section 'Stability versus change', the universe consists of 20 traits. Four of these are named, A, B, C and D. In the first simulation A and B are compatible, in the second A, B and C are all compatible, and in the third all four are compatible. The remaining trait pairs (including C and D in the first, and D in the second simulation) are set to be mutually compatible with probability 0.1, and otherwise they are mutually incompatible.

See data availability to access the code (in Python).

Data availability

The models used in this paper were implemented in Python. The program along with code to generate data for the figures are available in a Dataverse repository: https://doi.org/10.7910/DVN/KKDZX8.

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Notes

1 For some recent reviews of this interdisciplinary literature and the variety of empirical and theoretical methods employed, see Mesoudi, 2011, and Henrich, 2016.

2 While the cognitive capacity for such 'filters' would be genetically evolved, as cultural traits are acquired, they will be increasingly shaped by cultural evolution. However, this is not to discount the likely existence and relevance of innate biases that modulate and influence processes involved in cultural acquisition, innovation, and change. For some discussion of these issues, see Cowie, 1999, Sterelny, 2012, Lewens, 2015, and Heyes, 2018.

3 Losing a trait can represent different actions depending on what is being studied. An individual can forget a piece of information, lose a skill or a preference, or suppress the use and display of the trait (if the focus is on visible culture). If, for example, trait A is a preference for X and B a preference against it, then B replaces A.

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Competing interests

The authors declare no competing interests.

Additional information

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