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## Introduction

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# Foundations of cultural evolution

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## 1. Introduction

The field of cultural evolution is a very active and successful research area. The cultural evolution approach attempts to understand the dynamics and diversity of culture from an evolutionary perspective, from the small-scale transmission of cultural variants between individuals to the emergence of large-scale distributions of these variants. The idea that cultural change can be regarded as a process that is to some extent analogous to genetic change has spurred the introduction of a wide range of conceptual and methodological tools, often adapted from the toolkit of evolutionary biology. These diverse methods (from optimality models to psychological experiments and comparative analyses) are devised and employed by an equally diverse scientific community, with research backgrounds in disciplines like anthropology, archaeology, biology, economics, linguistics and psychology. The systematic use of mathematical models, evolutionary simulations, phylogenetic methods and model selection techniques to analyse large datasets distinguishes the field from more traditional cultural studies in the humanities and social sciences.

A steady number of specialized conferences, books and special journal issues (including a previous theme issue of *Philosophical Transactions B* [1]) testify to the attractiveness of 'cultural evolution thinking' and add to the general impression that cultural evolution has matured into a full-fledged interdisciplinary field. Yet, there are numerous foundational issues on which the cultural evolution community has not yet reached consensus. A small survey that we conducted among researchers from the cultural evolution community in preparation for this theme issue suggests substantial disagreement on various fundamental issues: whether cultural traits are analogous to biological replicators (45% agreed, 41% disagreed), whether the principles of genetic evolution largely apply to cultural evolution (44% agreed, 56% disagreed), whether models of cultural evolution must be rooted in mechanistic descriptions of cultural transmission (40% agreed, 53% disagreed), whether small-scale experiments can help explain larger-scale cultural patterns (53% agreed, 40% disagreed) and whether 'culture' in non-human animals is fundamentally different from human culture (48% agreed, 38% disagreed).

## 2. Foundational themes

From all this, we concluded that this is the right time to scrutinize the conceptual and methodological foundations of cultural evolution. To this end, we organized a workshop at the Lorentz Center in Leiden (Netherlands, April 2019), which formed the starting point of this theme issue. We identified three themes where foundational questions clearly arise.

- (i) What are the (often implicit) assumptions underlying models of cultural evolution? Are different modelling approaches mutually compatible? How can mechanistic views on cultural transmission be integrated in current models? How realistic are models of cumulative culture? Can models of cultural macro-evolution be integrated with models of micro-evolution? How can models be validated? Which approaches are best suited for generating testable predictions?

- (ii) How can findings from experiments produce robust knowledge about cultural processes? How is cultural transmission shaped by cognitive processes? How can we develop an integrative approach to cultural evolution in which both changes in mental representations and in behavioural expressions of culture are taken into account? To what extent are cultural processes determined by communication systems and institutional settings?
- (iii) What is the scope and what are the limitations of (phylogenetic) comparative methods for inferring cultural evolution processes? How robust are the conclusions of model-based approaches to infer patterns from processes (and vice versa)? To what extent have the various models been validated? Is there an objective way to identify units of cultural evolution? How can we quantify cumulative culture?

The first three parts of this theme issue correspond to the above themes of the Lorentz workshop. Most contributions were not written by workshop participants, but two articles [2,3] are ‘group reports’ that directly summarize insights obtained during the workshop.

One of the main goals of this theme issue is to stimulate cross-talk among modellers, experimentalists and researchers studying patterns in the field. This is important because the hypotheses that are tested by experiments are generated by empirical data as well as by mathematical models, and the assumptions of comparative approaches can only be rigorously tested by simulations and experiments. Moreover, many of the questions tackled by the cultural evolution community are closely related to topics traditionally covered by the humanities. We, therefore, have the additional goal of stimulating cross-talk with the humanities. To this end, part 4 of this theme issue presents papers by Leerssen [4] and Kronfeldner [5] who reflect on cultural evolution from a humanities perspective.

### 3. Modelling the dynamics of cultural change

The four articles in part 1 of this issue highlight contrasting aspects of cultural evolution theory. The contribution of Smolla *et al.* [2] critically evaluates the state of (theoretical) cultural evolution research. The authors discuss both the similarities of and the differences between genetic and cultural evolution, emphasizing some key differences that are currently still underappreciated. From this, they derive 12 major research challenges, thus providing directions for future research on the dynamics of cultural change.

Jansson *et al.* [6] tackle two of these challenges by scrutinizing the common modelling assumption that cultural traits are adopted and transmitted independently of each other. They argue that cultural traits are often closely interwoven and that the relationships between them are important as they affect both the transmission process and learning biases. The authors introduce a theoretical framework for studying the evolution of ‘cultural systems’ of interdependent cultural variants and employ a simulation model to illustrate how this systems approach changes predictions of cultural dynamics and outcomes.

The contribution of Mesoudi [7] discusses two processes that have figured prominently in debates on the nature of

cultural evolution and its underlying mechanisms: ‘cultural selection’ (selection-like social learning biases, such as the imitation of prestigious or successful individuals) and ‘biased transformation’ (cognitive processes that modify culturally acquired information in non-random and consistent directions). The author develops a set of models to illustrate how each process may impact the direction and outcome of cultural evolution in similar or different ways. He concludes that both cultural selection and biased transformation play important roles in cultural evolution, but that their relative importance is likely to differ between cultural domains.

The contribution of Kuijper *et al.* [8] presents a model that systematically investigates when social learning is favoured over other mechanisms as a means to obtain information about the environment. In doing this, the authors contrast social learning with a wide range of alternative ways of obtaining environmental information, including individual learning, maternal effects, and genetic and epigenetic cues. They demonstrate that horizontal social learning is highly adaptive in predictable environments, and further show that the type of environmental predictability (positive versus negative autocorrelation) determines which type of social learning is favoured (prestige biases versus conformity biases).

Currie *et al.* [9] discuss the role of institutions in cultural evolution. Institutions have a major impact on human culture: by determining the rules governing interactions and transactions; by coordinating behaviour; by organizing the transmission of cultural information and by imposing whole systems of cultural norms and beliefs. Yet, the institutional setting plays a minor role in most current models of cultural evolution. Importantly, institutions also change, but the laws governing this change are far from clear. The evolution of institutions may be considered cultural macro-evolution, while the evolution of culture within an institutional setting corresponds to cultural micro-evolution. It is still an open question whether cultural macro-evolution is governed by similar principles as cultural micro-evolution. Also to what extent is institutional change ‘adaptive’ in that evolved institutions guide human behaviour in a more favourable direction, such as favouring cooperation?

### 4. Unravelling the mechanisms underlying cultural evolution

The articles in part 2 focus on the role of mechanisms in cultural evolution. Because social learning is the mode through which cultural information is transferred between individuals, it has been a topic of intense focus in the field of cultural evolution. However, research has often been conducted on a high level of abstraction, focusing on the ways that information can be transferred and the ramifications of this transfer for the evolutionary process. This has led to a relative neglect of other (e.g. neural or cognitive) processes that underpin this information transfer. Aiming to correct this bias in perspective, Singh *et al.* [3] draw together evidence from diverse disciplines that point to the importance of other mechanisms (beyond social learning) for the understanding of the emergence of culture, the evolution of cumulative culture and the design of cultural traits. The authors have assembled a rich variety of studies, both on humans and other animals, that show how these largely

neglected mechanisms can significantly impact the evolutionary process. They argue that a wider perspective, including the full set of mechanisms (from neural to cognitive-behavioural to populational) adds explanatory power, leads to novel research hypotheses and opens up new avenues for cultural evolution research.

In line with this general plea, Perry *et al.* [10] emphasize the importance of investigating creativity and invention as a critical source of cultural variation and thus a driver of cultural evolution. Reviewing the literature on the role of the invention (mainly in non-human animals), the authors identify important factors that promote the creation of new ideas and practices and that play a decisive role in their spread or their loss. They discuss which circumstances elicit inventions, what kind of traits are most easily invented, which properties distinguish inventors from non-inventors and what population structures promote the rise and spread of inventions. By highlighting gaps in the empirical and theoretical literature, and by sketching ways how these gaps might be closed, the authors aim to inspire new research on the emergence, transmission and spread of cultural variation.

Birch & Heyes [11] outline a new, mechanistic theory for the evolution of cumulative culture. Human culture is unique in that small improvements to skills and technologies accumulate, resulting in products of such complexity that no single individual could possibly have designed them on their own, without learning from others. Such fast cultural accumulation draws on a suite of cognitive mechanisms (e.g. selective learning, language, mind-reading), and only humans have evolved sophisticated versions of these mechanisms. The authors propose that these unique human capacities are the result of a self-reinforcing process of ‘culture–culture coevolution’. In other words, the cognitive mechanisms underlying cumulative culture are themselves a product of cultural evolution. This ‘self-assembly hypothesis’ provides a novel perspective on the origins of the psychological and cognitive processes underlying cultural evolution and challenges traditional views based on gene–culture coevolution.

Morin *et al.* [12] review experimental studies on the extent to which people use social information in updating their beliefs and behaviours, a process lying at the heart of cultural transmission. Their synthesis of results from a wide range of different research traditions reveals a consistent pattern of people heeding social information less than theoretically predicted. The authors discuss current proximate and ultimate explanations of such ‘egocentric discounting’ and suggest ways forward to deepen our understanding of this pervasive phenomenon.

## 5. Deciphering the patterns of cultural variation

The contributions to part 3 address a major challenge for the field of cultural evolution: to infer the unknown history of cultural change from cultural patterns. A diverse set of phylogenetic comparative methods, often adapted from evolutionary biology, are increasingly being used to identify the drivers of trait-change over time. These methods can be very powerful and illuminating, yet their application is not without pitfalls. Evans *et al.* [13] discuss the scope and the limitations of applying phylogenetic methodologies to cultural data, thereby providing recommendations for their

appropriate use. In particular, the choice of phylogenetic methods and models requires a careful consideration of the nature of the traits to be studied, and the inclusion of multiple lines of evidence.

Lukas *et al.* [14] discuss the usefulness of phylogenetic simulations for scrutinizing the validity of phylogenetic models and methods. By applying their simulation approach to empirical datasets, the authors demonstrate that the interplay of various factors (such as gaps in the data, the shape of the phylogenetic tree, properties of the cultural traits, the mode of cultural transmission) can strongly influence phylogeny-based inferences. Their simulation tool offers the cultural evolution community a handle to assess how, and to what extent, properties of the sample, the phylogeny and the cultural traits affect the reliability of tree-based conclusions.

Teixidor-Toneu *et al.* [15] explore the usefulness of the phylogenetic approach in an interdisciplinary setting. The authors test if relatively recent ethnobotanical data can be used to trace back ancient plant knowledge in the Nordic countries. Phylogenetic inferences of ancestral states are evaluated against historical, linguistic and archaeobotanical evidence. The authors demonstrate how quantitative and qualitative data analysis can integrate diverse kinds of evidence. Their contribution highlights both the promise and challenges of interdisciplinary data collection and interpretation in cultural evolution.

## 6. Cross-talk with the humanities

Part 4 leaves the stage to scholars that do not self-identify as cultural evolutionists. Their research and questions offer an opportunity for cultural evolutionary self-reflection. Kronfeldner [5] wields philosophical tools to justify the view that cultural inheritance is truly distinct from biological inheritance. To dig these separate channels of inheritance, she calls upon the autonomy of cultural change, the near-decomposability of culture (meaning that cultural elements interact more among themselves than with biological elements) and on differences in temporal order between cultural and biological inheritance.

In an invitation for dialogue, Leerssen [4] explains how the historical human sciences view ‘culture’ and cultural change: self-reflexive, complex, with ‘form’ (‘etic’ components) and ‘meaning’ (‘emic’ components) inextricably linked. This view contrasts with perspectives from cultural evolution that focus on culture mainly as a system of information storage and transfer. How then, Leerssen asks, is it possible for these fields to meet if their outlook on the very essence of culture is so fundamentally different? His answer is surprisingly positive and opens up new perspectives.

This theme issue has brought together disparate perspectives on the foundations of cultural evolution, fostering dialogue from scholars both within and beyond this vibrant field. We are thankful to the contributors that have taken up the challenge of addressing various foundational issues, scrutinizing common modelling assumptions, probing the mechanisms of cultural transmission and critically evaluating established methods for the analysis of cultural variation. We hope that this issue helps solidify the conceptual foundations of the field of cultural evolution, and that it promotes interdisciplinary collaborations to study the dynamics and diversity of culture.

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**Competing interests.** We declare we have no competing interests.

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