



Thesis report: The influence of social processes and structures on cultural evolution

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This thesis studies cultural evolutionary dynamics, with a particular focus on socio-cognitive processes that might affect this process. The thesis consists of an impressive seven chapters in addition to the general introduction and discussion, which comprise a mix of experiments (chapters 1,4,6), computational modelling (chapters 2,3,5), and a review (chapter 7).

The introductory chapter provides a good overview of the state of knowledge, focusing on social learning, culture, cultural evolution, and the relationship between cultural evolution and social structure and/or demographic processes. It is relatively brief, but overall, as the chapters are all written as papers with their own included introductions, an extensive introduction would be unnecessary. The thesis is also cohesive enough that the introduction can, and does, focus on the key concepts. However, I would note that it could have devoted more time to the study system in question, and why it is a good choice of model system for the thesis topic.

Chapter 1 then experimentally examines the effect of turnover on the rate of cultural evolution. It does this by creating replicate groups in captivity of a small passerine known for social learning, great tits. Using a now classic paradigm (the two-direction door puzzlebox) a new behaviour (pushing a door left) was introduced across all groups. Pushing the door right was more efficient, the experiment compared the times until the group switched in static vs groups experiencing replacement of individuals. Groups experiencing turnover were faster to switch to more efficient traditions, with modelling revealing the underlying driver (e.g., naïve immigrants were more able to sample the behavioural space).

This is a simple, elegant experiment that is aimed at answering one long-standing question, and has such, has a potentially wide impact across multiple disciplines. This work has been published in *Current Biology*, and is an important contribution to the literature, already subject to a dispatch in that same journal. In addition to its scientific contribution, it represents a large amount of work (several months across two winters), and incorporates several cutting-edge methodologies to maximise the data output (e.g., remote bar-code tracking of individuals). It is perhaps the most outstanding chapter of this thesis.

Chapter 2 makes the argument that current models for learning and social transmission don't fully capture the feedback between social learning, reinforcement learning and social transmission. To examine this, Michael therefore creates a generative model that combines approaches from two existing inferential social learning models; EWA



(Experience Weighted Attraction) and NBDA (Network-based diffusion analysis). He then uses these to test how divergences in acquisition and production of behaviour could affect the cultural diffusion dynamics. This work has recently been accepted for publication at *Proceedings of the Royal Society B*, and in my opinion, is a strong theoretical contribution to the field of cultural evolution. Similar to Chapter 1, its strength lies in the simple, yet impactful, insights it generates.

Chapter 3 is an agent-based model, that uses the insights generated from Chapter 1 and 2 to ask how turnover may affect cultural evolution across a broad range of parameter space. This work finds that information loss is a critical mechanism linking turnover to beneficial cultural evolution. This chapter demonstrates a new set of skills from the previous two chapters, and is a valuable extension to that work, while remaining very cohesive with those previous chapters. The results will be potentially relevant for both human and non-human animal studies.

Chapter 4 uses the experimental set-up developed in Chapter 1 to ask a new question – what happens when knowledgeable individuals migrate between groups, and how is this effected by changes in the resource or environmental landscapes? The experiment reveals an additive effect, with birds most likely to switch to match their new group's tradition when the resource and physical landscape changes. Overall, this suggests an important effect of environmental cues on triggering social learning, potentially helping to explain the maintenance of culture diversity across groups.

Similar to Chapter 1, this chapter represents a huge amount of work encompassing two field seasons. This is commendable in itself, but it is also really exciting to see the novel methods and analytical techniques developed in previous chapter applied to this work to gain new insights into the underlying cognitive mechanisms of learning. This chapter is perhaps less polished than the other chapters, but I suspect it will generate an exciting publication.

Chapter 5 is another model, this time asking focusing on the link between cumulative cultural evolution and social structure. Here, Michael works with two other co-first authors to ask about the effect of social network architecture on speed of recombinatory cultural evolution. This study builds on previous models in the human cultural evolutionary literature, and as such, helps to expand the scope of the thesis. It is a solid piece of work, that, while perhaps not generating ground-breaking insights by itself, definitely furthers the literature. It is also already published in *Proceedings of the Royal Society B*. Interestingly, this chapter is extremely collaborative, as are the final two chapters. Science is no longer a lone endeavour, and it is extremely important that scientists learn to work collaboratively. It is nice to see this reflected in this thesis.

Chapter 6 is another collaborative chapter, consisting of a re-analysis of an experimental dataset collected in 2017. This experiment built on the classic sliding puzzle-box paradigm (also used in chapters 1 and 4), and add a second step, in order to ask whether cultural



evolution to increasing complexity can occur in great tits. This is a nice complement to the experiment in chapter 1 that examined cultural evolution to increasing efficiency, and fits very well into the overall theme of the thesis. It also gives the opportunity for the inclusion of wild data, again as a nice complement to the more controlled captive experiments. This chapter is also already published, in the *Philosophical Transactions of the Royal Society B*.

Chapter 7 is a review of the CCE literature, focusing on the literature in non-human animals. It develops the idea that the drive towards increasing efficiency is likely to be widespread, and as such is likely to be a key component in the evolution of cumulative culture. By bringing in individual-level reinforcement learning as a key, but neglected aspect of animal culture, it neatly ties this review into the insights gained from the empirical chapters. This work is already published in the same special issue as the previous chapter, in the *Philosophical Transactions of the Royal Society B*.

Finally, the general discussion reflects on this and develops these themes. After summarizing the chapters, it discusses their findings in relation to two main topics – the effect of social processes and of social structures on cultural evolution. Under these subheadings, it clearly lays out the main insights gained from this thesis. While it highlights the main areas needing further investigation, it would have been nice to see some more specific recommendations for future projects in these areas. I hope this is a topic we can hear more about in the defense, as it is clear Michael has developed a unique and clear perspective on this topic throughout this thesis.

In summary, this is an absolutely outstanding thesis. It presents a remarkable seven distinct and well-developed chapters, four of which are already published in highly regarded journals. The chapters showcase a range of skills, from experiments on captive and wild birds, to generative models, agent-based modelling, to theory driven reviews. The thesis also showcases Michael's ability to work both independently and collaboratively, while maintaining a clear voice. Indeed, while all chapters form important and distinct contributions to the literature, they also all speak to the same thematic goals, of understanding how social processes and structures influence cultural evolution (whether towards efficiency or complexity). Overall, these cohesive and overarching themes allow the thesis to have a clear narrative, and to generate novel insights into this important topic.

Grade: 0

Sincerely,

Dr. Lucy Aplin