UNDERSTANDING HUMAN CULTURE: THEORETICAL AND EXPERIMENTAL STUDIES OF CUMULATIVE CULTURE

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I, Elena Miu, hereby certify that this thesis, which is approximately 57,000 words in length, has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for a higher degree.

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Contributions

Chapter 2

The Second Social Learning Strategies Tournament was designed by Luke Rendell and Kevin Laland, with additional input from Sam Bowles, Robert Boyd, Magnus Enquist, Kimmo Eriksson, Marcus Feldman, and Richard McElreath. Luke Rendell, Stuart Murray, and Laurel Fogarty coded and ran the simulations, and collated the output. All other work and analyses were carried out by myself.

Chapter 3 & 4

The collection of the data was performed prior to the beginning of this project by Ned Gulley and the MathWorks team. Ned partly collated the output, and provided advice and information in support of the analyses. All other work is my own.

Chapter 5

The online interface used for the experiment in Chapter 5 was designed by myself, with input from Luke Rendell and Liam Haig. The online platform was built by Liam, in collaboration with Ned Gulley and Michael Broshi. All other work was carried out by myself.

General abstract

There is something extraordinary about human culture. The striking complexity of our technologies, institutions, beliefs, and norms has allowed us to colonise the entire planet. One aspect in which human culture is unique relates to its cumulative nature – we accumulate and build on knowledge from the previous generations, leading to incremental improvement in skill, which allows us to produce technologies no one individual could have invented on their own. Understanding the drivers and dynamics of this type of cumulative culture is essential for understanding how human culture has interacted with human evolution. This thesis is concerned with precisely that, and uses a mixture of theoretical and experimental approaches linking individual-level decisions to population-level processes in cumulative culture contexts.

Chapter 1 provides some essential background information. In Chapter 2 I used an agent-based simulation model to show that refinement, or incremental improvement in cultural traits, can lead to a drastic decrease of cultural diversity at the population level. This pattern was confirmed using experimental data from a collaborative programming competition in Chapter 3, where I showed that in a cumulative setting, the differential riskiness of copying and innovation drives participants to converge on very similar solutions, leading to a loss of cultural diversity. In Chapter 4 I explored individual differences in social learning strategies, finding considerable variation in how individuals rely on copying, with more successful individuals being more exploratory. I found that successful individuals had more influence on subsequent entries, which is consistent with a prestige bias. Finally, Chapter 5 addressed the link between group structure, diversity, and cumulative improvement. I found that larger groups accumulate more improvement than smaller groups, but smaller groups can also inhibit the convergence patterns we witnessed in larger groups, suggesting an optimal level of connectivity responsible for cumulative improvement.

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Chapter 1

Introduction

1. Introduction

Humans have been incredibly successful at colonising practically the entire planet, and this success relies to a large extent on our cultural abilities. Useful innovations and technologies spread through social learning, were maintained and improved over time, becoming more and more crucial to our survival in unfamiliar environments. Today, we depend on technology so complex that no one individual could invent in their entire lifetime, to the point that we would be helpless without it (Boyd and Richerson, 1985; Tomasello, 1999). There is little doubt that culture has contributed to our ability to adapt to different environments (Richerson and Boyd, 2005; Mathew and Perreault, 2015; Henrich, 2016), which raises the question of why humans differ so much from every other animal species in our overwhelming reliance on cultural learning.

This puzzle has only come more into focus in recent years as some scientists have increasingly argued that we are not the only species to show culture. Evidence has been steadily accumulating over the past 50 years pointing to the fact that many species show behavioural patterns shared between two or more individuals, which persist over time and are acquired through learning from other individuals (Fragaszy and Perry, 2003). From instances of circumstantial evidence of milk-bottle opening in birds (Fisher and Hinde, 1949; Hinde and Fisher, 1951) and sweet potato washing in Japanese macaques (Kawamura, 1959; Kawai, 1965), to examples from black rats (Terkel, 1995), dolphins and whales (Rendell and Whitehead, 2001), chimpanzees (Whiten *et al.*, 1999), orangutans (van Schaik *et al.*, 2003), and capuchins (Perry *et al.*, 2003), the evidence ensures the issue of animal culture is currently a very active field (Allen *et al.*, 2013; van de Waal, Borgeaud and Whiten, 2013; Aplin *et al.*, 2014).

Nonetheless, few argue that the kind of culture we see in humans is qualitatively equivalent to the culture we see in other non-human species. Other species, for instance, learn skills from each other, maintain those skills over generations, and show group differences in the way they use those skills that cannot be attributed to ecological or genetic variation, but these skills do not seem to change much from one generation to the next. Humans, on the contrary, accumulate and build on previous generations' knowledge, which leads to an improvement in skill and an increase in complexity. Is it this type of cumulative culture, producing a "ratcheting" in complexity of skill, which is specific to humans (Boyd and Richerson, 1985; Tomasello, Kruger and Ratner, 1993; Kurzban and Barrett, 2012). The question of why cumulative culture is so rare when there is ample evidence of cultural processes in more and more species is therefore key to understanding what makes humans unique.

The field of cultural evolution, stemming from the idea that cultural change can be described using the Darwinian principles of evolution, is concerned with answering questions about why the ability for culture evolved, how cultural systems change over time, what explains the patterns of cultural diversity we witness, and, ultimately, how and why human culture is unique (Mesoudi, 2011b). Cultural evolution took off as a field once it was formalised mathematically in the 1980s by Cavalli-Sforza and Feldman, and Boyd and Richerson, using theoretical models adapted from biology to investigate the conditions under which culture is expected to evolve, based on the premise that culture is beneficial and shaped by natural selection (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985).

In the past 20 years the field has flourished, and while mathematical modelling still guides much of the work (Henrich and Boyd, 1998; McElreath *et al.*, 2005; Enquist and Ghirlanda, 2007; Rendell *et al.*, 2010; Fogarty *et al.*, 2017), methodological approaches have extended to include laboratory experiments testing the predictions of those models (Caldwell and Millen, 2008; Kirby, Cornish and Smith, 2008; Mesoudi, 2008; Derex, Godelle and Raymond, 2013; Morgan *et al.*, 2015), as well as studies testing predictions using real data from the field (Henrich and Henrich, 2010; Hewlett *et al.*, 2011; Berl and Hewlett, 2015). Additionally, studies using phylogenetic comparative methods have been used to reconstruct evolutionary relationships between cultural traits such as languages (Atkinson *et al.*, 2008; Pagel, 2009; Dunn *et al.*, 2011), cultural artefacts (Tehrani and Collard, 2002; Tehrani, 2013; O'Brien *et al.*, 2014), or social norms (Jordan *et al.*, 2009;

Kushnick, Gray and Jordan, 2014). Finally, comparative studies have been used to investigate the cognitive differences between humans and other non-human species (Horner *et al.*, 2006; Pike and Laland, 2010; Dean *et al.*, 2012). This mix of theoretical and empirical methods, investigating questions ranging from how individual-level decisions interact in micro-evolutionary settings, and how in turn these translate into macro-evolutionary patterns over long periods of time, puts the field of cultural evolution in a unique position, spanning multiple disciplines concerned with the evolution of human behaviour, that allows multiple strands of evidence to connect in painting a still complicated picture of a complex phenomenon (Mesoudi, 2011b). This thesis similarly combines theoretical and empirical approaches to understand individual-level and population-level patterns relating to cumulative culture, which for the purposes of this work is defined as the incremental accumulation of knowledge over generations that leads to technologies that no one individual could have invented in their own lifetime, and results in patterns of descent with modification. This definition reflects closely Boyd and Richerson's position on culture (Boyd and Richerson, 1985), but a discussion of alternative interpretations will follow in subsequent sections.

1.1. Why humans?

Why is human cumulative culture so different from anything else we see in other animal species? Various explanations have been put forward, ranging from cognitive differences, social structure and demographic factors, and the dynamics of cultural evolution itself (see Dean *et al.*, 2013 for a review). Some of the influential theories suggest that humans are unique in the way they preserve culture from one generation to the next, and this fidelity of transmission is essential for maintaining useful information in a population and building on it (Boyd and Richerson, 1985; Tomasello, 1999). Tomasello (1999) goes even further, suggesting fidelity of transmission is crucially supported by understanding intentionality in other individuals, thus putting theory of mind at the core of cumulative culture.

Alternatively, increased sociality in humans would provide individuals with more opportunities for observation and learning (Pradhan, Tennie and van Schaik, 2012). Studies of modern hunter-gatherer societies seem to support this view, indicating that sociality could be a key factor leading to the evolution of cooperation (Apicella *et al.*, 2012), or even cumulative culture (Hill *et al.*, 2014). Another theory suggests demographic factors like population density, social organization, and intergroup competition, rather than complex cognitive mechanisms, might be key in explaining cumulative culture (Henrich, 2004; Powell, Shennan and Thomas, 2009; Kline and Boyd, 2010). Finally, the emergence of human culture might not be due to a single factor like a sudden cognitive development or drastic change in population structure, but could rather be the result of an interplay of multiple factors, small adaptations magnified at the population level, interacting and co-evolving through time over many generations to drive humans into the radically distinct cultural regime we witness today (Morgan *et al.*, 2015). Most of the cultural evolution field indeed takes this view (Richerson and Boyd, 2005; Henrich, 2016; Laland, 2017), studying how population-level processes magnify small individual biases, how learning biases and cultural traits reinforce each other and co-evolve, to the extent that cultural becomes an additional inheritance system, co-evolving with genetic inheritance.

1.2. Comparative studies of cumulative culture

Comparative studies of culture are generally concerned with identifying the cognitive similarities and differences between humans and other non-human animals that would contribute to our differences in culture. A first suggestion regarding these differences stems from the observation that humans tend to learn through imitation, for example accurately copying bodily movement while making a tool, while non-human primates seem to rely on emulation, or focusing on the results of another’s actions without faithful replication of the process required to achieve those results (Tomasello, 1996; Legare, 2017).

This is further supported by humans’ apparent tendency to ‘over-imitate’, or imitate functionally irrelevant actions. Children readily imitate irrelevant actions both in an opaque puzzle task and in a transparent task, in which it is obvious which actions are required for solving the puzzle. Chimpanzees, on the other hand, arguably rationally imitate all actions in the opaque condition, but stop imitating irrelevant actions in the transparent condition (Horner and Whiten, 2005). Children over-imitate even when specifically instructed to only copy relevant actions, when the social pressure is diminished, under competition, and under time constraints (Lyons, Young and Keil, 2007; Flynn, 2008; Lyons *et al.*, 2011), and over-imitation seems to occur even in adults (Flynn and Smith, 2012). However, this phenomenon breaks down when children are copying their peers (Flynn, 2008), or when the actions appear unintentional (Lyons *et al.*, 2011). It is still unclear whether over-imitation is driven by a human predilection for imitation, so strong that it becomes the default way to learn even when in situations when it is not necessary, or whether over-imitation is the result of a higher social motivation in humans, which manifests even in experimental settings (Heyes, 2012b).

Whiten et al. (2007) suggest that the explanation for the human-chimpanzee difference in culture might be attributed to behavioural conservatism. Chimpanzees can learn socially and sustain traditions within groups (Whiten *et al.*, 2007), yet in a study using a honey-dipping task that could be solved using two techniques, the second more complex, but more rewarding, chimpanzees failed to switch to the second technique, persisting in using the first technique they had acquired (Marshall-Pescini and Whiten, 2008). This result is not isolated (Hrubesch, Preuschoft and van Schaik, 2009; Gruber *et al.*, 2011), and a more recent comparative study sheds some light on the differences between humans and primates in terms of cumulative culture (Dean *et al.*, 2012). The authors presented children, chimpanzees, and capuchin monkeys with an equivalent puzzle box that could be solved at three levels of difficulty, each more difficult, building on the previous one, but more rewarding. Results indicate that humans, but not the other two groups, manage to advance successfully to higher levels because of a package of socio-cognitive mechanisms such as teaching, imitation, and pro-sociality.

Several authors propose that signs of cumulative culture are present in other species apart from humans, giving examples of tools that seemingly increase in complexity used by chimpanzees and New Caledonian crows (Boesch, 2003; Hunt and Gray, 2003), or the use of the same tool in a more efficient way in chimpanzees (Yamamoto, Humle and Tanaka, 2013). While there is convincing evidence that the maintenance and use of these tools are culturally mediated, the history of the development of the tools is unknown, and therefore it is unclear whether they have been the product of a genuine cumulative cultural process in which the newer and more efficient versions of the tool are built through incremental improvement on older versions. Using controlled experimental approaches involving transmission chains, two studies have shown that repeated learning in other species can lead to an increase in efficiency (Sasaki and Biro, 2017) or learnability (Claidiere *et al.*, 2014), but not the combination of efficiency and complexity that typically characterises cumulative culture. Therefore whether cumulative cultural evolution is a uniquely human process remains an open question.

1.3. Studies of social learning

Social learning, or learning influenced by contact with other individuals (Heyes, 1994), is essential for spreading beneficial behaviours in a cultural species. Intuitively, social learning should be advantageous when it allows bypassing the cost of trial-and-error learning, and indeed the entire cultural evolution field is based on the assumption that social learning is beneficial and shaped by natural selection. At the core of this is the idea that social learning is adaptive and has been selected for in cultural species, and much of the early work in the field has focused on identifying the conditions under which social learning would evolve. Although intuitive, the benefits of social learning over individual learning are not immediately obvious (Boyd and Richerson, 1985; Rogers, 1988; Giraldeau, Valone and Templeton, 2002; Enquist and Ghirlanda, 2007; Rieucau and Giraldeau, 2011).

An important starting point in the theoretical study of social learning was a simple though experiment designed by Rogers (Rogers, 1988), who simulated a population of social and individual learners in a changing environment. In this context, social learning does not increase the mean population fitness. When social learners are rare, most individuals learn through trial-and-error, accurately sampling the environment and collecting useful information, so social learning provides cheap and beneficial information. As social learners increase in frequency, the number of individuals sampling the environment and collecting accurate information decreases. As the environment changes, social learners increasingly copy out-dated information (Feldman, Aoki and Kumm, 1996). The population thus reaches equilibrium when both social learners and asocial learners coexist with the same average fitness.

Rogers' paradox, then, is the surprising result that social learning does not seem to be adaptive compared to individual learning. The solution to this apparent conundrum lies in allowing individuals to adopt a flexible strategy that involves selective use of both social and asocial learning (Boyd and Richerson, 1995; Kameda and Nakanishi, 2003; Enquist and Eriksson, 2007; Rendell, Fogarty and Laland, 2010), which, it seems, is something that most humans also employ (Mesoudi, 2008). For instance, Enquist and Eriksson propose a learning approach called critical social learning, where individuals use social learning as a default, but switch to asocial learning if they fail to acquire the adaptive trait, thus outcompeting pure social learners and pure individual learners (Enquist and Eriksson, 2007). Indeed, evidence from experimental studies indicates that humans do selectively switch between strategies while completing social transmission tasks (Mesoudi, 2008, 2011a), though some studies find a polymorphism, with people exhibiting individual differences in their use of social learning (Kameda and Nakanishi, 2002; Efferson *et al.*, 2008).

Thus, in a changing environment, individuals should use specific rules, 'social learning strategies', which dictates the circumstances under which individuals should exploit information from others, and who they should learn from (Laland, 2004; see Rendell et al., 2011 for a review of both the theoretical and experimental literature). These rules specify when an individual should copy (for instance, 'copy when uncertain', 'copy when dissatisfied'), what cultural traits they should copy, and which individuals they should focus on. A distinction was made between context biases, like frequency-dependent biases, in which case the identity of the trait copied depends on how frequent it is in the population, conformity being a prime example, and content biases, like payoff-bias, in which case the identity of the trait copied depends on how beneficial it is inherently (Laland, 2004). It has been argued that payoff-bias would be cognitively costly, as it requires that individuals accurately assess how beneficial a trait is, while a conformist bias could be used as a heuristic easily applicable by a naïve individual – if most individuals do X, X could be a useful thing to do (Boyd and Richerson, 1985; Henrich and McElreath, 2003).

A great deal of the modelling work was concerned with understanding the circumstances under which these social learning biases would be adaptive and expected to evolve (Henrich and Boyd, 1998; Schlag, 1998; Eriksson, Enquist and Ghirlanda, 2007; Nakahashi, 2007; Kendal, Giraldeau and Laland, 2009), but virtually all these studies investigate social learning strategies independently, without attempting to pit them against each other and compare their relative influences. In contrast, Rendell et al. did just that (Rendell *et al.*, 2010). The authors organized a computer tournament in which academics and members of the public submitted strategies that competed against each other in a complex, changing environment. These strategies specified how individuals in a population choose between social and individual learning. This tournament method, pioneered by Axelrod & Hamilton in a study on co-operation (Axelrod and Hamilton, 1981), injects a dose of realism compared to the simple mathematical models mentioned above, and allows the assessment of the relative advantages of a large number of different social learning strategies. Results showed that social learning is beneficial under a much greater range of conditions than previously thought – the winning strategy used copying almost exclusively when learning. In this context, learners do not have to rely on complex computation in order to identify the beneficial behaviours, because the burden of selectivity is carried out by their models. Agents are rational, performing their best behaviour from those they have learned in order to achieve optimal payoff, with the result that demonstrators are effectively filtering their behaviour, such that copiers are exposed to and learn adaptive traits without having to evaluate themselves the payoffs. This conclusion was surprising in light of ‘Rogers’ paradox’ discussed before, but these insights were only made possible by the design of the tournament, which models individuals and their interactions rather than merely looking at average population behaviour.

Empirical studies have confirmed that humans make use of both payoff bias and conformist bias in their learning (McElreath *et al.*, 2008; Mesoudi, 2011a; Morgan *et al.*, 2012), and results generally seem to indicate people have a stronger preference for payoff bias when given the choice. Although much rarer, field studies also bring evidence for social learning strategies in more naturalistic settings. For example, in fishing villages in Fiji, pregnancy food taboos are learned preferentially from prestigious unrelated older women (Henrich and Henrich, 2010). In the lab McElreath et al. used a simple task in which participants learn to choose between two crops to maximise their payoff, one of them giving higher yield. Participants could access the crop choices and the yields of their group members. By fitting several theoretical models to the population-level empirical data, the authors found support for a strategy that relies strongly on payoff bias. This approach of trying to infer learning mechanisms from population-level patterns of spread is debatable (Kandler and Steele, 2009), and a single study (Morgan *et al.*, 2012) found evidence of conformity, as defined by Boyd and Richerson, in humans (i.e. disproportionate tendency to copy the majority; Boyd and Richerson, 1985). Fish (Pike and Laland, 2010) and birds (Aplin *et al.*, 2014) also display apparently conformist behaviour, suggesting social learning strategies are not restricted to humans.

Much of this work assumes individuals do not vary in their use of social learning strategies, but interestingly, Molleman et al. (2014) found consistent individual differences in how participants rely on social information, with some individuals having a stronger preference for payoff information, while others showing stronger preference for trait frequency information. Even more, the relative reliance on trait frequency information depends on the task. In a best choice context, participants have a stronger preference for payoff information, but they display a stronger preference for frequency information in a social dilemma or coordination game, where the individual payoff depends on the behaviour of the other participants. This work provides intriguing evidence that people use social learning strategies flexibly and strongly dependant on context, but also show consistent individual differences in social learning, which persist over time and over contexts (Mesoudi *et al.*, 2016).

The same authors find, in a separate study, that not only do humans show consistent individual differences in their use of social learning strategies, these different learning strategies affect the outcome of social interactions (van den Berg, Molleman and Weissing, 2015). Frequency-bias learners proved more co-operative in a social dilemma task than payoff-bias learners, which also led to frequency-biased learners accumulating higher payoff. Combined with the results before, these findings suggest that indeed the efficiency of individual differences in social learning approaches is modulated by context. Even more, individual preferences for social learning vary with subsistence style – populations of independent pastoralists show less reliance on social learning than horticulturalists, for which reliance on co-operation with a larger number of unrelated individuals is more important for survival (Glowacki and Molleman, 2017), and seem to be mediated by the cultural individualist – collectivist distinction (Mesoudi *et al.*, 2015). This reiterates the point that moving away from theoretical models in which only single social learning strategies are investigated can show surprising interactions that question our assumptions.

Social learning strategies are essential for the study of cultural evolution because they determine which cultural traits are selected and spread in the population, and have deciding effects on population dynamics of cultural evolution. Conformist bias has been suggesting as a key element supporting cultural group selection (Henrich and Boyd, 1998), as this relies on selection on variation between groups. Conformity is a mechanism that leads to behavioural homogeneity within groups and behavioural heterogeneity between groups, thus being able to stabilise behaviour within group while maintaining variation between groups. Intuitively, this type of blind copying of the majority should be advantageous for spreading beneficial behaviours, but would also hinder the spread of adaptive innovations and even cumulative culture (Eriksson, Enquist and Ghirlanda, 2007), yet of course a conformist bias would not be used indiscriminately. If individuals are allowed to use social learning strategies flexibly, conformist learning would be useful after a migration event, for example, or when the individual is behaviourally naïve (Boyd and Richerson, 1985).

The accumulation of beneficial information relies on two key elements: beneficial traits arise through innovation in the population, which subsequently selects these beneficial traits and improves on them. Payoff bias is therefore essential for accurately identifying the cultural traits worth learning and preserving in the population and therefore crucial to cumulative culture (Mesoudi, 2015). When direct information about payoffs is unavailable, indirect cues for success, like prestige, can be used to guide social learning (Henrich and Gil-White, 2001). Much of the modelling work regarding cumulative culture has assumed individuals are capable of easily identifying the most beneficial traits, and has instead focused on this second element of selection and preservation, paying particular attention to the importance of fidelity of transmission, which will be discussed in the following section.

1.4. Models for studying cumulative culture

Much of the earlier modelling work that has set the foundation of the field of cultural evolution was concerned with which conditions can support the evolution of the ability for culture, particularly the type of cultural phenomena we witness in humans. Boyd and Richerson (1985, 1996) emphasise that the type of culture they talk about involves an accumulation of knowledge over many generations that leads to technologies that no one individual could have invented in their own lifetime. This has since become a trademark of cumulative culture, and scholars interested in identifying the roots of cumulative culture in other species often invoke this inability for individual invention as a criterion for establishing whether the phenomenon observed qualifies as cumulative culture. Tomasello, mainly interested in the cognitive mechanisms supporting this accumulation and particularly the preservation of culture, illustrates cumulative culture as a “ratchet”. For him, the essential feature is that cumulative culture allows the population to accumulate and maintain knowledge through an irreversible process in which cultural traits cannot be lost (Tomasello, 1999). Another view which has received great attention portrays cumulative culture as a package of cultural traits that can be learned without needed to fully reproduce each step of its invention – in a way, one does not need to track the ontogeny of a trait to be able to learn it and use it, but this also means cultural traits can be easily lost along with the knowledgeable demonstrators (Henrich, 2016).

A mixture of historical factors and differences in the focus of study has led to a confounding diversity of definitions for 'cumulative culture', which sometimes leads to unproductive debate. Nonetheless, early modelling studies were clear in the type of phenomena they were trying to address. In their earlier work, Boyd and Richerson plainly state:

> "*Culture increases average fitness if it makes the learning processes that generate new knowledge less costly or more accurate. [...] social learning allows learned improvements to accumulate from one generation to the next. When learning in small steps is less costly per unit improvement in fitness than learning in large steps, the cumulative learning over many generations can increase average fitness*" (Boyd and Richerson, 1995)

Therefore, they do not just specify the conditions under which they expect culture to emerge, but also how this culture is meant to operate. The authors do not question the fact that improvement takes place incrementally, in small steps, and leads to a pattern of descent with modification very similar to biological evolution – this is indeed something that has been witnessed again and again in the evolution of technology, in patterns of scientific discovery (Basalla, 1988), and in the archaeological record (Shennan, 2011).

Boyd and Richerson (1996) found that natural selection favours culture when individual learning is costly or error prone, and the environment is moderately variable. If environments are stable, organisms can adapt genetically to environmental conditions. If environments change too fast, culture would not be beneficial since individuals would socially learn information that becomes out-dated very quickly. Is it at intermediate levels of environmental variation that culture excels, as it proves a faster way of adjusting than genetic adaptation. The authors find through a theoretical model that the rarity of cumulative culture can be explained through a frequency dependent differential benefit of culture. When culture is rare, most of the behaviours that can be learned socially are behaviours that an individual could invent alone. Once cumulative culture takes off, the accumulation over generations leads to behaviours much more beneficial than anything one individual could invent on their own, thus dramatically increasing the benefit of social learning. This explains why cumulative culture is rare, but does not explain what it was that initially drove the emergence of culture.

Macro-evolutionary models provide useful broad-stroke results essential for guiding further work, but more specific, more realistic modelling forces us to formally define and question our assumptions. Moving from population-level modelling to individual-level modelling allows us to investigate how individual interactions affect the broad patterns witnessed, but it also requires us to be more specific, in this case, about our assumption regarding what cumulative culture is and its mechanistic underpinnings. One of the first studies to take an individual-level approach to modelling cumulative culture operationalized this phenomenon as a two-step process. An individual socially learns the traits known by its randomly chosen cultural parent, and then innovates a random number of traits. Thus this model investigated the accumulation of traits in the population and its relationship to population size and learning efficiency, showing that the expected amount of culture increases with both those factors (Strimling *et al.*, 2009).

Most of the theoretical work concerned with cumulative culture focuses on the increase of the number of traits in the population, or on the monotonic accumulation of improvements in a single trait. In an attempt to go beyond such simple representations of culture, Enquist, Ghirlanda, and Eriksson (2011) used a modelling framework where the state of culture at any time point depends on the previous states, thus incorporating a measure of interaction between cultural traits that is so clearly characteristic of human culture. They emphasise the dependencies between cultural traits as a key characteristic of cumulative culture, and investigate how different dependency models affect the amount and diversity of culture. They present the first attempt in the modelling literature to capture dependencies that describe not only refinement or progress, but also differentiation, combination, substitutability and loss of cultural elements. The authors showed that these different dependency frameworks resulted in very different patterns of evolution in terms of both the rate of growth of the number of elements in the population and the diversity of independently evolved cultures. For example, stepwise modification lead to linear growth in the amount of culture, while differentiation lead to faster, exponential, growth and combination lead to even faster growth. At the same time, modification lead to relatively similar cultures, while cultures based on differentiation and combination ultimately grew to be very different. This is a crucial point for the rest of this thesis – we expect that different processes involved in cumulative culture will lead to different population patterns.

1.5. The role of fidelity of transmission in cumulative culture

The accumulation of useful knowledge depends on the rate of innovation, and the spread of that innovation (Boyd and Richerson, 1996). If individuals innovate, but these innovations fail to be recognised and picked up by the population, cultural accumulation is impossible. Therefore, the population needs to be able to identify, spread, and maintain innovations through generations, and it has been argued that it is in the fidelity with which knowledge is transmitted through generations that human uniqueness lies. Much of the original modelling work concerned with cumulative culture consists of macro-evolutionary models that focus on the importance of the fidelity of transmission to the emergence and maintenance of cultural accumulation (Enquist and Ghirlanda, 2007; Enquist *et al.*, 2008, 2010; Lewis and Laland, 2012). For example, Enquist and Ghirlanda (2007) use a mathematical model of the accumulation of adaptive and maladaptive traits in a population to show that adaptive filtering is essential for the accumulation of adaptive traits, again suggesting that individuals need to be able to correctly identify and accurately copy the beneficial traits in order for cumulative culture to evolve.

The importance of transmission fidelity is also emphasised by a modelling study comparing the rates of innovation, modification, combination, and trait loss (i.e. a proxy for fidelity). The authors show that, by far, fidelity is the most important factor in maintaining cultural accumulation and diversity (Lewis and Laland, 2012). This raises questions about why fidelity of transmission is higher in humans, and what type of mechanisms we could be using to support this faithful preservation of information. In addition to the imitation-emulation debate, one popular suggestion is teaching (Tomasello, 1999; Fogarty, Strimling and Laland, 2011; Castro and Toro, 2014; Laland, 2017) – by this argument, humans are the only species that purposefully and altruistically alter their behaviour to facilitate learning in conspecifics based on an understanding of knowledge differences rooted in theory of mind (sometimes termed ‘intentional teaching’, as a contrast to ‘functional teaching’, which we are not the only species to do; Thornton and Mcauliffe, 2014). A more elaborate alternative suggests that, through niche construction, humans have crafted an environment that makes cultural learning easier (through artefacts, for example), and have evolved cognitive tools (like language) which facilitate social learning (Sterelny, 2011; Morgan *et al.*, 2015).

1.6. The importance of population size for cumulative culture

The interplay between the fidelity of transmission and population size has been explored by several studies with similar results (Mesoudi, 2011c; Aoki, Wakano and Lehmann, 2012; Kempe, Lycett and Mesoudi, 2014; Nakahashi, 2014; Acerbi, Tennie and Mesoudi, 2016), but it is one specific study that has been most persuasive in definitively establishing population size as a crucial factor for cumulative culture. Henrich developed a model that investigated the conditions under which skill in a population can accumulate and get lost, guided by the case of Tasmanian technology loss. When Tasmania became cut off from the Australian mainland around 10,000 years ago, the population lost a collection of useful complex skills and technologies, like winter clothing and boomerangs, and the author argues that this loss is due to a decrease in effective population size that resulted from the cut-off (Henrich, 2004).

In this model, individuals in a population could accurately identify and attempt to copy the best skilled individual. Learning is error-prone though, and a parameter of the model determines the variation in this individual copy error. In line with how difficult cumulative cultural skills are, most of the time, when attempting to copy, individuals will not manage to reach the best skill level in the population. Nonetheless, through lucky accidents or successful innovations, a small proportion of individuals will acquire a higher skill level, thus improving the overall population skill level. Thus, over time through repeated improvements on the best skill, the population cumulatively advances in skill. The key finding here is that the change in skill depends on the population size. The more individuals there are, the higher the chance that someone will improve the highest skill. The converse of this is that, as the population size decreases, so does the probability of beneficial learning errors, which means that after a certain threshold the population begins losing skill rather than accumulating it, which, Henrich argues, is what explains the Tasmanian scenario.

Henrich's model relies necessarily on the assumption that individuals can accurately identify and copy the best skilled individual in the population. This assumption, as the discussion of social learning strategies above has shown, is far from trivial. This study was not without its critics (Henrich, 2006; Read, 2006, 2009), but it proved nonetheless influential, and has since been adopted and modified to investigate questions related to population structure, migration, overlapping generations, and different social learning strategies (Powell, Shennan and Thomas, 2009; Bentley and O'Brien, 2011; Lehmann, Aoki and Feldman, 2011; Mesoudi, 2011c; Vaesen, 2012; Kobayashi, Ohtsuki and Wakano, 2016). Similar models have been fitted to archaeological data, indicating that the appearance and disappearance of complex technologies in the Palaeolithic coincides with demographic changes (Shennan, 2001; Powell, Shennan and Thomas, 2009).

The main criticism of Henrich's model is that it does not incorporate population structure. Individuals have cheap unconstrained access to the best model, but once population density or connectedness patterns change, the spread of an innovation will cease to be as straightforward. A model distinguishing between population size, network size, and connectedness (i.e. in this case, distinguishing between total population size, the number of individuals in a subpopulation that are available for copying, and the number of links between subpopulatons) finds that total population size has little effect on cultural accumulation, but network size and connectedness do (Baldini, 2015). This works emphasises the importance of population structure in the diffusion of information, which, in turn, affects the accumulation of skill. The effect of population connectedness on cultural accumulation is probably more salient than the effect of population size, and indeed this observation has been confirmed empirically (Derex and Boyd, 2016).

The importance of population connectivity for human culture has also been emphasised by Muthukrishna and Henrich (2016), who suggest that useful innovations do not arise as a result of the exceptional cognitive capabilities of isolated geniuses, but rather as an interaction between ordinary human psychology and population connectedness. According to the authors, connected populations produce collective brains, and the bigger and more connected the population, the higher the rate of innovations. This is confirmed in urban areas – urban density predicts the rate of innovation (Carlino, Chatterjee and Hunt, 2007), and so does the population of cities, when innovation is measured in patent numbers (Bettencourt *et al.*, 2007). What is more, too much connectivity can lead to decrease variance, which would lead to a lower rate of useful recombination, thus suggesting there is an optimal amount of interconnectivity that leads to the highest innovation rate.

Although not many studies have investigated this relationship using data from real populations, the ones that do show mixed results. Some studies support a positive relationship between complexity and population size (Kline and Boyd, 2010; Collard, Ruttle, *et al.*, 2013), while others find no evidence (Collard, Kemery and Banks, 2005; Collard, Buchanan, *et al.*, 2013). For example, island population size predicts the size of the fishing toolkit in the Pacific (Kline and Boyd, 2010), but there is no link between population size and technological richness in hunter-gatherers from Western North America (Collard, Buchanan, *et al.*, 2013). Empirical evidence from the experimental laboratory also points to the fact that larger group size promotes higher improvement in skill or better preservation of skill at the micro-evolutionary level (Caldwell and Millen, 2010; Derex *et al.*, 2013; Muthukrishna *et al.*, 2013; Kempe and Mesoudi, 2014), but it is unclear whether the same processes that support better task performance in the laboratory also explain macro-evolutionary processes in real world populations.

There is mixed evidence that links population size to measures of language complexity (Nettle, 2012). Population size is also related to the word rate of change – languages with larger speaker populations gain words faster and lose words slower in the basic vocabulary (Borenstein, Feldman and Aoki, 2008). Nonetheless, while the evidence points to a positive relationship between speaker population size and phoneme inventory size, the relationship is negative with morphological complexity. Language complexity is an intricate issue though, as languages vary on several dimensions in the way they encode information, with trade-offs between these dimensions, which might confound any relationship with population size.

Similarly, in a study investigating the relationship between population size and the complexity in a non-technological domain, folktales, the authors found mixed results (Acerbi, Kendal and Tehrani, 2017). There was a significant positive relationship between population size and complexity measured as the overall number of folktale types, but a negative relationship with complexity measured as the number of tale motifs. This mixed result could be attributed to the fact that different levels of cultural complexity depend to varying degrees on population size because they are subject to different pressures, just like language is shaped by both expressivity and learnability. Alternatively, the authors suggest that the relationship between population size and complexity could be domain dependent. For a functional domain like technology we expect a strong relationship, yet a domain like folktales, which is not subject to functional pressures, but in which instead cultural traits can be easily individually reproduced without a need for strong replicative transmission, should show a weaker dependence on population size.

1.7. Empirical studies of cumulative culture

The study of cumulative culture draws on historical work on the study of the evolution of technology (Basalla, 1988), but was kick-started by theoretical modellers, and a large body of literature has accumulated over the past 30 years, centred on population-level factors supporting the emergence, maintenance, and spread of culture. While individual-level modelling can test how our assumptions about individual cognition and how individual decisions translate into population-level patterns through the dynamics of cultural transmission, these assumptions need to be corroborated by experimental studies investigating real humans. Much of the recent work still relies on theoretical approaches, yet the past 10 years have witnessed a boom in the number of empirical studies on cumulative culture, aimed to test theoretical results in the laboratory, as well as take cumulative culture research into more realistic settings.

In a highly influential empirical study of cumulative culture, Caldwell and Millen (2008) used a micro-society paradigm, which simulates generational transmission by repeated replacement of individuals, in order to establish what information is needed to be transmitted in order to deliver skill improvement over generations. The authors used simple tasks like building a paper airplane or building a tower out of spaghetti and clay, with a clear measureable goal like how far does the airplane fly or how tall the tower is. Participants were paired, with one building, and the other one observing. After a fixed period of time the observer became the builder, and the builder was replaced by a naïve observer. Results show that the artefacts improve over time throughout the chains, and chains show patterns of descent with modification – designs are more similar within chains than between chains. Both these features are characteristic of cumulative culture.

This transmission-chain paradigm has been used by the same authors to test questions about whether this kind of improvement necessarily requires imitation or whether the same accumulation can be achieved merely using product information (i.e. participants only need to be exposed to the artefact and do not need to witness the making process). The authors conclude that imitation is not necessary for improvement in skill (Caldwell and Millen, 2009). This study has however been criticised for using tasks that are too simple and transparent – cumulative culture involves copying complex, opaque artefacts that reap payoffs that are hard to judge (Muthukrishna *et al.*, 2013), and using a transparent task that participants can solve alone arguably says little about the mechanisms underlying cumulative culture. Indeed, research using more complex tasks actually shows that only product with no process information is not sufficient to lead to cumulative improvement in other laboratory settings (Derex, Godelle and Raymond, 2013; Wasielewski, 2014).

From a comparative perspective, this same transmission chain method has been used to show that pairs of pigeons find increasingly more efficient flight routes between two points (Sasaki and Biro, 2017). Over several generations, the authors replaced each experienced pigeon in a pair with a naïve pigeon and show that, compared to pigeons navigating alone and pigeons navigating in fixed pairs, the naïve pigeons in the experimental condition actually stabilised on more efficient routes. Although showing a decrease in performance at the beginning of each generation, pairs consisting of one experienced and one naïve pigeon managed to overtake the other two groups. The authors argue that a type of collective intelligence operating by pruning less efficient routes out of a larger collection of ‘innovations’ contributed by the larger pool of participants can lead to this incremental improvement in skill, and provocatively claim this is an example of non-human cumulative culture. Arguably however, this study illustrates an increase in efficiency, but not complexity, the latter also being one of the purported characteristics of cumulative cultural evolution, and the debate about whether these results really do represent cumulative culture looks set to continue along similar lines to the debate about animal culture in general.

The same transmission chain framework has been adapted to more complex tasks like using an online interface to build virtual fishing nets that vary on a series of dimensions, which interact in opaque ways to give a payoff that cannot be easily deduced from the building process (Derex, Godelle and Raymond, 2013), or tasks like using complex graphics software to replicate an image, or even real-world knot tying (Muthukrishna *et al.*, 2013). These methods, as mentioned above, were used to explore questions regarding the cognitive mechanisms necessary for cumulative improvement, finding that for such more complex tasks mere product information is not sufficient for cultural accumulation. The same methods were used to test the link between group size and improvement, confirming theoretical results.

1.8. Open questions

The emphasis on increasing efficiency and complexity as defining criteria for cumulative culture stems from the long-lasting focus on the field on the evolution of technology (Basalla, 1988). The study of evolution in cultural domains that differ in functionality sheds doubt on the definite position of efficiency and complexity at the heart of cumulative cultural evolution. For instance, transmission chain studies of language evolution show that artificial languages change over time to be more learnable (Kirby, Cornish and Smith, 2008), which in some cases can mean less complex. Participants were asked to learn an artificial language that randomly associated visual stimuli varying on three dimensions (shape, colour, movement) with novel labels. Results show that through repeated communicative interactions, the languages became more efficient, as indicated by the participant success in communication, but also more learnable, as the languages became more structured – for example, different parts of a word referred to each of the three dimensions the objects differ on.

This interplay between learnability and communication efficiency is not a uniquely human phenomenon and has been shown, through similar methods, to arise in baboons (Claidiere *et al.*, 2014) and zebra finches (Fehér *et al.*, 2017). This increase in structure through iterated learning emphasises how individual learning biases become magnified in the population through repeated interaction between individuals, but also bears testament to the fact that once culture serves more than a straightforward functional purpose (as it was the case for technology), it becomes more difficult to predict how incremental accumulation over time will shape cultural traits. In the case of language, communicative efficiency could be considered an equivalent of tool efficiency, but the additional constraint of learnability means that languages will evolve to be simple enough so they can be easily learned, but complex enough to be able to express meanings effectively, and structure is a solution to this compromise. What this means, though, is that language complexity can be measured on different dimensions. Certainly learnability plays an important part in the evolution of functional culture and technology needs to be successfully passed on from one individual to another and will therefore be structured by this pressure. Yet the difference between language and technology is that technology relies to a large extent on material culture that can be copied directly and thus supports the transmission of more complex culture, which means that the pressure for learnability is lower. Similarly, symbolic culture is shaped by different pressures than functional culture, and we expect different processes to affect how culture is transmitted and changes over time (Morin, 2015).

In addition to giving empirical validity to theoretical predictions, experimental studies of cumulative culture allow us to observe what other factors not yet formally investigated might contribute to cultural accumulation. Modelling work typically pits social learning against individual learning, assuming copying is a purely replicative process, but Muthukrishna et al. (2013) for example observe that when presented with several models, people actually combine information from different sources instead of faithfully replicating a single one. Similarly, Derex et al. (2015) found that participants combined and transformed information from multiple sources in order to produce new solutions. A study of innovation in US patents also finds that combination is a key process involved in innovation (Youn *et al.*, 2015). These observations emphasise the idea that multiple processes may be at work to support cumulative cultural evolution. The lines between innovation, modification, refinement, combination, and replication can become blurred and, importantly, different processes might produce different diffusion patterns, and might interact with population structure differently. For example, an emphasis on combining traits means group connectivity can crucially affect the spread of information and decisively affect the accumulation of skill in a population (Derex and Boyd, 2016).

Much of this work also illustrates that results regarding cumulative culture are task-dependent. Different problems emphasise different factors that contribute to cumulative improvement and, naturally, experiments are an effective means of isolating these different factors and testing their effects. Nevertheless, we are only beginning to develop intuitions about the different aspects relevant to cumulative culture and how they interact, and more complex, more naturalistic experimental scenarios that allow participants to engage freely in a cumulative task are sorely needed.

1.9. Thesis outline

In summary, the uniquely cumulative character of human culture has been studied using theoretical and empirical approaches, both in human and non-human animal populations. Key findings emphasise the importance of faithful transmission, as well as the crucial significance of population size, for the accumulation and maintenance of culture. This body of literature bears testament to the importance of the combined effort of theoretical and empirical methods for elucidating big questions about the evolution of human behaviour. More recently, evidence has been accumulating suggesting that relaxing our assumptions regarding the homogeneity of populations can have important effects on the dynamics of cultural evolution and, potentially, on how culture accumulates. This is a key point that this work will be addressing, by exploring the patterns of cultural evolution though both theory and a realistic microcosm of cumulative culture, and asking questions regarding the importance of different processes involved in cumulative culture, like refinement and recombination. I will also be investigating the effects of individual social learning strategies approaches on cumulative culture, as well as the importance of group structure and population size for the dynamics of cumulative culture.

In **Chapter 2** I investigate a key process involved in cumulative cultural evolution, the incremental refinement of behaviours, through a complex realistic agent-based model that extended the Social Learning Strategies Tournament (Rendell *et al.*, 2010). This will answer questions regarding how refinement is used effectively in a complex exploration-exploitation problem, how the use of refinement changes under different learning and environmental conditions, and how it affects population patterns of cultural diversity in the population.

The remaining three chapters of this thesis focus on a complex task, a collaborative programming competition, which simulates cumulative cultural evolution in a more realistic context than ever attempted in the empirical literature so far. In **Chapter 3** I examine the drivers and dynamics of cumulative cultural evolution in this context, answering questions about the patterns of similarities and improvements of cultural artefacts over time, their effect on cultural diversity, and the importance of copying and recombination in cumulative culture.

Chapter 4 is concerned with individual differences in the cumulative setting of the programming competition. Here, I explore whether different learning approaches with regards to social learning are related to improved performance both at the individual level and at the population level. This will contribute to the recently emerging literature on how individual differences in social learning strategies affect cultural population patterns and reiterate the importance of recognising the value of investigating heterogeneous populations for the evolution of culture. In **Chapter 5** I extend the programming contest paradigm experimentally to investigate how group structure and group size affect cumulative improvement and cultural diversity, adding to the population size – cumulative culture debate and exploring potential mechanisms underlying the effect of population size on cumulative culture. Finally, in **Chapter 6** I discuss the results from a broader perspective, considering the wider implications for our understanding of cumulative cultural evolution.

Chapter 2

Cumulative Culture and Cultural Diversity in the Second Social Learning Strategies Tournament

Abstract

Human culture, which allows us to build and improve on knowledge from previous generations, has contributed to the extensive adaptability of our species, but we have yet to find definite answers regarding the trade-offs between innovation and copying in a cumulative cultural setting. I introduce a computer tournament in which participants submitted strategies that specified how to learn socially and asocially in a complex, changing environment, and focus on the cumulative extension, in which individuals can invest in improving behaviours they already know. I find that this type of cumulative culture creates a scenario in which the population benefits from a level of refinement much higher than what is individually beneficial, which creates clear tensions between individual and population interests. Thus, individual refinement is costly, while copying is cheap, which leads to a strong convergence in the population on a very limited number of extremely long-lived refined behaviours. Additionally, I see evidence that strong convergence is associated with success in the tournament. This raises the question of what other processes besides refinement are responsible for the remarkable diversity that cumulative cultural evolution displays.

2.1. Introduction

Culture is responsible for the extraordinarily diverse behavioural repertoire that has led to our species' impressive adaptability (Mathew and Perreault, 2015). Social learning, learning influenced by contact with conspecifics (Heyes, 1994), is at the heart of spreading beneficial knowledge, and is used by an extensive variety of species. Nevertheless, it is still unclear why social learning is profitable and how best to copy.

Intuitively, social learning should be beneficial when it allows individuals to bypass the cost of trial-and-error learning. For example, learning which type of mushroom is edible by trying out different varieties is very risky, while simply choosing the mushrooms you have seen other individuals eat is easy and effective. The story is obviously not this straightforward, and indeed theoretical studies have questioned the benefits of social learning (Boyd and Richerson, 1985; Rogers, 1988; Giraldeau, Valone and Templeton, 2002; Enquist and Ghirlanda, 2007; Rieucau and Giraldeau, 2011). For instance, some theoretical studies suggest that social learning in a changing environment is only beneficial when it is rare in the population (Rogers, 1988). In a mixed population of individual and social learners, when most of the population is learning through trial-and-error, sampling the environment and collecting accurate information, social learning provides good information quickly and cheaply. Evolution, however, would then lead to an increase in the proportion of social learners. As fewer and fewer individuals learn by trail-and-error, there will be fewer who sample the environment in an effective manner. Copying in this context will most likely provide unreliable, out-dated information (Feldman, Aoki and Kumm, 1996; Rendell, Fogarty and Laland, 2010). The population, therefore, will reach equilibrium on a mixture of social and asocial learners, both with equal fitness.

This implies that copying others indiscriminately is not adaptive and, indeed, further work suggests that individuals should use social learning selectively (Kameda and Nakanishi, 2003; Enquist and Eriksson, 2007; Rendell, Fogarty and Laland, 2010). Both humans and non-human animals employ social learning strategies, which specify how, what, and under what circumstances individuals should copy (Laland, 2004; see Rendell et al., 2011 for a review of both the theoretical and experimental literature). This body of work has mainly focused on general analytical models that explore a very small subset of strategies. In order to explore a large range of alternative social learning strategies in a complex, changing environment, Rendell et al. (2010) organised a computer tournament, a method previously used to investigate the evolution of cooperation (Axelrod and Hamilton, 1981). This involved participants submitting various strategies that specified when to use individual and social learning, which then competed against each other in an agent-based simulated environment. The main result of the tournament was that social learning proved beneficial under a much broader range of conditions than previously shown, even when copying was highly imprecise. The competitive dynamic of the tournament lead individuals in the population to always exploit their best behaviours, effectively filtering the information. Therefore, social learners did not need to be as selective when copying, because the other individuals were selective in what they made available to copy.

If we are interested, though, in what makes human culture unique, one key point is the fact that our culture relies on accumulating knowledge and behaviours from previous generations, allowing for gradual incremental improvement in skill (Boyd and Richerson, 1996; Tomasello, 1999). This type of cumulative culture relies crucially on an interaction between innovation and copying. Each generation needs to acquire and maintain the skills and knowledge gained so far in order to pass them on (Enquist *et al.*, 2010), yet at the same time enough novelty needs to be generated in order to allow for the improvement in the skills inherited from previous generations. As a result, this type of cultural evolution allows for a remarkable accumulation of traits in the population, such that individual cultural repertoires are smaller because no one individual can learn and know all of the traits. It leads to such advanced technologies that no one individual could have invented on their own. It involves adding, modifying, refining, and combining cultural traits, which influence each other and interact in complex ways.

Cumulative cultural evolution is a large-scale, long-term, elaborate process, which makes it difficult to study. Nevertheless, to date, an extensive literature consisting of both theoretical and experimental approaches has shown that population size, population structure, and transmission fidelity all favourably affect the accumulation of culture, but most of this work has focused on a limited set of conditions. The modelling literature has typically investigated population level dynamics and has been defining cumulative culture as either an increase in the number of traits (Enquist *et al.*, 2008; Strimling *et al.*, 2009), improvement in a single trait (Henrich, 2004; Mesoudi, 2011c; Nakahashi, 2014) or, even more generally, the persistence of one trait in the population (Enquist and Ghirlanda, 2007; Enquist *et al.*, 2010). More recently, modellers have started to investigate how this type of cultural accumulation takes place when traits provide the user with a fitness benefit, which increases with increased refinement (Mesoudi, 2011c; Ehn and Laland, 2012; Lewis and Laland, 2012), finding similar results regarding the interaction between population structure and the fidelity of transmission.

In laboratory studies, transmission chain methods have been used to simulate intergenerational transmission, aiming to investigate how one skill such as building spaghetti towers (Caldwell and Millen, 2008), fishing nets (Derex, Godelle and Raymond, 2013), or arrowheads (Derex *et al.*, 2015) improves over time. This body of work was mainly concerned with questions regarding the type of information required for successful improvement in such tasks over generations, and the importance of group size to this end. Results indicate that more complex tasks require more extensive information regarding the artefacts and the processes required to build these artefacts, as well as requiring larger groups to sustain higher accumulation or lower cultural loss. More recently, the focus has been extended to more specific processes involved in cumulative culture, like recombination of increasingly beneficial skills (Derex and Boyd, 2015, 2016), but more work in this direction is sorely needed.

One study points out the importance of different ways of conceptualising cumulative culture in modelling approaches (Enquist, Ghirlanda and Eriksson, 2011). The authors used a complex framework that allows for interaction between cultural traits in order to investigate how different modes of cultural dependency, such as sequential improvement, differentiation, and recombination, affect cultural accumulation. Results showed that these different processes produced very different patterns of cultural evolution in terms of the rate of growth of the number of cultural traits in a population, and the diversity between populations. Therefore, different innovative processes involved in cumulative culture can lead to different population patterns. However, the modelling literature has largely exclusively focused on sequential improvement, using simple theoretical populations.

Clearly, modelling something as complex as cumulative culture requires drastic simplification, but by focusing on specific aspects we can gain a better understanding of how each contributes to the emergence and evolution of the phenomenon. Previous studies have mainly been concerned with investigating cumulative culture one process at a time, focusing primarily on cumulative culture as successive sequential improvement in one trait, which leaves more nuanced sources of cumulative improvement largely unexplored. What is more, the methodological approaches could be updated to more complex, more realistic systems.

One such more realistic approach is the Social Learning Strategies Tournament (Rendell *et al.*, 2010) mentioned above, a complex agent-based simulation in which individual agents use elaborate learning strategies and interact directly in a changing environment. The Tournament investigated the basic trade-off between social and individual learning, but this paradigm provides an excellent opportunity for investigating cumulative culture. I introduce here the Second Social Learning Strategies Tournament, which extended the first in three directions (1) by allowing individuals to choose who to copy from, (2) by allowing individuals to invest in improving a behaviour they already know, and (3) by allowing for migration between subpopulations. In the model bias extension, individuals are allowed to choose whom they want to learn from, using information like age, number of offspring, and mean lifetime performance. The spatial extension introduces migration between three populations, thus allowing for a spatially structured meta-population.

Finally, in the cumulative extension, individuals are given the option to invest in improving already known behaviours in order to increase their payoffs.

This chapter will be concerned with analysing data from the cumulative extension, in which cumulative culture is modelled in terms of refinement. Refinement here is defined as an incremental improvement of several independent cultural traits. This definition does not distinguish between whether the repeated improvement is the result of the effort of a single individual or whether it is a collective endeavour, but in practice the simulations ran for much longer than an individual lifespan, which resulted in incremental improvement from numerous generations. There is currently no consensus in the literature about whether cumulative culture is purely a collective process or whether the same results could be achieved by a theoretically immortal single individual, so our model of refinement here captures a combination of both individual and collective improvements. The richness of the tournament model allows us to ask new questions about cumulative culture. For example, much of the work mentioned above focused on identifying the conditions under which social learning is beneficial relative to individual learning, but to our knowledge little work has directly compared the benefits of refinement against individual learning and, importantly, copying. The data from the tournament easily allows us to do that and answer questions like what strategies do we expect to be selected for choosing when to copy, when to innovate something completely new, and when to work on improving what you already know? For cumulative culture to evolve, some individuals need to invest time in improving already known solutions – but who does that, and when? Finally, this framework allows to link small-scale individual decisions to population-level patterns of behaviour. This work adds more realism to models like the one by Enquist et al. (2011), and answers questions about whether refinement can lead to specific population-level patterns of culture that we would not expect in populations where cumulative improvement is not possible.

Therefore this chapter will focus on the dynamics of refinement at the individual and population level in the tournament. More specifically, in the sections that follow I will begin with a general overview of the tournament setup. The large scale of the tournament framework allows us to investigate how the use of refinement changes in different environmental conditions. The first results section is concerned with how the use of refinement changed across the parameter space, investigating how refinement was affected by environmental change, the number of models, the probability of failure, and the maximum level of refinement level. I expect that more refinement will be associated with a higher number of models, as the information and implicitly refined information would spread faster, which is in line with previous work linking population size and cumulative culture. Similarly I expect that more refinement should be associated with higher environmental change, as cumulative culture should provide a quick way of adapting to fast-changing environments, and it should be associated with a higher accuracy of transmission as the fidelity of transmission has been posited as crucially important to cumulative culture.

The second section answers questions regarding how much refinement took place and the benefits of refinement at the strategy level for performance in the tournament. I expect differential fitness to be associated with refinement at the individual and population level, as refinement is beneficial for the population but not for the individuals, which should create tensions between individual and population level interests. Finally, the last section shifts the focus to population level dynamics, and is concerned with how refinement affected cultural diversity. As individuals invest in beneficial refinements, the population should converge on these refined behaviours, which should decrease cultural diversity. Because these three sections deal with relatively unrelated topics, I included a separate description of the methodology at the beginning of each section, along with short discussions when relevant. A general discussion concludes this chapter.

It is worth noting that this dataset was the result of a large collaborative project. I was not involved in the design, not in the data gathering, but all the analyses are my own.

2.2. Tournament specifications

Participants submitted *strategies* to enter the tournament. Each strategy was a set of rules specifying how agents should behave in an agent based simulation on the acquisition and use of knowledge. The strategy details when agents should in each iteration or round of a simulation choose to either make use of a behaviour they already know (through a move called EXPLOIT) or learn asocially (using INNOVATE), socially (OBSERVE), or invest in improving a behaviour they already know (REFINE).

The tournament was based on a restless multi-armed bandit problem (Schlag, 1998; Gross *et al.*, 2008). The ‘one armed bandit’, or the slot machine, involves pulling one arm in order to receive a payoff drawn from a given distribution. In our case, the bandit had 100 arms. This means there was a choice between 100 behaviours, each associated with a payoff drawn, here, from an exponential distribution, so that most payoffs were small, but some were very high. In addition, the bandit was restless: the payoffs changed over time. Each round, with a certain probability, the payoff of each behaviour changed independently, being replaced with a new payoff drawn from the same exponential distribution. The aim of each agent was to learn which behaviours are best to use (i.e. which of the bandit’s arms to ‘pull’) and when in order to maximise its lifetime payoff.

This was an exploration – exploitation problem: agents first needed to learn how to pull an arm either though social or asocial learning, and could then exploit that arm to receive payoff. This established a trade-off between learning and exploiting - the cost of a learn move was that it could have been an exploit move that reaps payoff: an opportunity cost. Since evolutionary ‘fitness’ in the simulation depended on the accumulation of payoff, agents should exploit as much as possible, but in order to make sure they were exploiting the best behaviours, they needed to balance exploit with smart learning.

The simulated environment contained a population of 100 agents, each controlled by one of the strategies submitted by our participants. The agents engaged in a turn-based interaction over 10,000 time steps. At each time step, each agent performed a move. The first move they could select, EXPLOIT, involved choosing a behaviour in their repertoire and reaping its payoff – this was the only move that allowed for the accumulation of payoff. On the other hand, INNOVATE allowed agents to learn a behaviour selected at random from the set of 100 possible behaviours not in their repertoire yet. By 'learning a behaviour' in this case I mean adding that behaviour to the agent's repertoire, along with exact information about the behaviour's payoff. The third move available was OBSERVE, which allowed agents to learn randomly chosen behaviours from the set of behaviours the other agents were exploiting at this time step. A simulation parameter, $n_{observe}$, controlled how many other individuals the agent could observe – if $n_{observe}$ was higher than 1, the agent learned all the $n_{observe}$ behaviours observed, along with information about their payoffs. OBSERVE moves were associated with errors both in terms of acts and payoffs. Each of the $n_{observe}$ acts could fail being copied with probability $p_{copyFail}$, which was a parameter of the simulation – if the copying failed, no information regarding the behaviour or the payoff was added to the agent's repertoire. Additionally, when copying was successful, the payoff information was not exact – an error term drawn from a Poisson distribution was added to the payoff estimate, which ensured that the higher the payoff observed, the larger the error around the estimate.

It is worth noting that the payoff information acquired along with a behaviour related to the state of the environment at that particular time. If the environment changed, the agents would possess out-dated information. This payoff information could, however, be updated in two ways. When an agent chose to play EXPLOIT, the payoff it received was used to update the payoff recorded in its repertoire; similarly, if an agent OBSERVED a behaviour it already knew, the payoff information of that behaviour was updated with the current value observed.

Evolution was implemented through a death-birth process. At each time step, agents died with probability of 1/50 (giving each agent an expected lifespan of 50 rounds), and were replaced with the offspring of survivors. The probability of reproduction was proportional to the mean lifetime payoff, which was defined as the total payoff acquired (through EXPLOIT moves), divided by the number of time steps they had been alive for. Agents were born behaviourally naïve, but they inherited their parent's learning strategy. At birth mutation occured also with probability 1/50, which meant that instead of inheriting the parent strategy, offspring could inherit a strategy selected at random from the set of strategies competing in the simulation. These mutations were how strategies appeared in populations initially containing a single strategy, and did not occur in the last quarter of each melee contest (see below).

To summarise, each simulation round consisted of the following steps: (1) each agent was chosen sequentially to play a move, until all agents had played, (2) some individuals died, and individuals reproduced with a probability proportional to their mean lifetime payoff, (3) the environment changed with a probability p_c, which was a parameter of the simulation, and (4) in the spatial extension, some individuals migrated between populations.

In the cumulative extension, agents could use an additional move, REFINE. Each behaviour was associated with a refinement level, which was initially zero when the behaviour was learned through INNOVATE. A REFINE move allowed agents to choose a behaviour in their repertoire and increase its refinement level. The payoff of a behaviour, in the cumulative extension, was the sum of the basic payoff defined by the environment, plus a refinement increment. Therefore, increasing the refinement level of a behaviour increased the payoff associated with that behaviour by a certain increment, which was proportional to the refinement level. When a refined behaviour was copied through OBSERVE, the refinement level was also copied. Individuals did not know the refinement level of acts they have in their repertoire – only that the refinement level increased by 1 – and learned a new total payoff available for that act, without error. Importantly, this increment was independent of the environmental variation – even if the basic payoff of the behaviour changed, the increment remained constant.

Parameter summary:

p_c – probability of environmental change

$n_{observe}$ – number of individuals copied by an agent playing OBSERVE

$p_{copyFail}$ – probability that copying failed for every act OBSERVED

r_{max} – in the cumulative extension, this was the maximum allowed refinement level.

The refinement increment that was added to a behaviour's payoff was a function of r (the current refinement level, ranging from 0 to the maximum possible level, r_{max}) and r_{max} itself, plotted below, and given by:

$$i = \left[\left(\frac{0.05}{1-0.95^{r_{max}}}\sum_{j=1}^{r} 0.95^{r-j}\right)p_{max}\right] \qquad \text{(Equation 2.1)}$$

where p_{max} was the maximum possible increment, defined as the mean of the basic payoff distribution, multiplied by 50. The payoff increment i is plotted as a function of the refinement level r in Fig. 2.1 below.

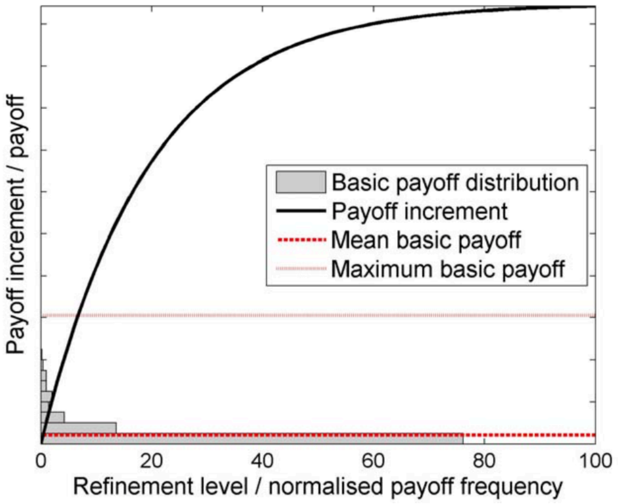


Figure 2.1 – relationship between refinement level and refinement increment. The payoff increment, in black, is compared to the mean and maximum basic payoff values. The shape of basic payoff distribution is plotted on a different scale using the gray bars for illustrative purposes

Refining a given behaviour enough times means the refinement increment would surpass even the highest possible basic payoff. Bearing in mind that this increment did not change when the environment did, this translated into refining the population 'out' of environmental variation. Therefore once the population crossed this threshold into a world in which refined behaviours are the only behaviours worth knowing, individuals only needed to do enough learning to acquire a well enough refined behaviour, ideally through copying. A smart refiner did not even need to refine at all – as long as they found themselves in a refined environment, they just needed to learn the refined behaviour from someone else.

The tournament was run in three stages:

Stage 1: Single extension pairwise

For each extension, all 51 strategies entered in the tournament competed against each other in a round-robin pairwise fashion with only that respective extension active and possible (i.e. a cumulative round, a model-bias round, and a spatial round). Each contest between strategies A and B involved seeing if strategy A could invade a population using strategy B, and vice-versa. In each simulation, a population of the dominant 'defender' strategy was introduced, and ran for 100 rounds in order to establish behavioural repertoires. Then, the second 'invader' strategy was allowed to mutate in. Each such contest was replicated with 6 sets of parameters, twice with strategy A invading B, and twice with B invading A, for repeatability. The score of a strategy in each simulation was the frequency of that strategy in the population in the last quarter of the simulation (i.e. the proportion of agents in the population using strategy A or B). The score of a strategy in each extension was the average score of that strategy across all the simulations it was involved in. The parameter values chosen for these runs were $p_c = \{0.001, 0.01, 0.1\}$, $n_{observe} = \{1,5\}$, $r_{max} = 100$, $p_{copyFail} = 0.05$.

Stage 2: Single extension melee

For each single extension pairwise contest set, the strategies that scored within the top ten in that extension proceeded to stage 2, where they all competed against each other simultaneously, with only that respective extension active. The strategies were allowed to invade through mutation a standard defending strategy, *innovateOnce*, which learned once asocially and then exploited that one behaviour for the rest of its life. Again, the score of a strategy in each simulation was the frequency of that strategy in the population in the last quarter of the simulation. The winning strategy for each extension was the strategy with the highest average score within that extension contest set.

The second stage was run as two sets of simulations: one using parameter values drawn systematically from fixed sets of values, with 10 replicates each, and one drawing parameter values from plausible distributions, to preferentially explore the more biologically realistic regions of the parameter space.

The systematic parameter values used were:

$p_c = \{0.001, 0.005, 0.01, 0.05, 0.1, 0.2, 0.4\}$

$p_{copyFail} = \{0, 0.01, 0.05, 0.1, 0.15, 0.25, 0.5\}$

$n_{observe} = \{1, 2, 5, 10\}$

$r_{max} = \{10, 25, 50, 100, 500, 1000\}$

Stage 3: All extensions melee

Finally, the top 5 strategies from each single pairwise melee extension were chosen to compete against each other in a melee fashion, with all three extensions active simultaneously. Score was calculated as above, and the strategy with the highest score was designated the final winner of the tournament. Like Stage II, this involved running simulations using a set of fixed parameters that was identical to the ones used in Stage II, each repeated 5 times, as well as simulations using parameters drawn from random distributions.

2.3. How does refinement change across the parameter space?

2.3.1. Methods

In order to quantify how refinement changed across the parameter space, I illustrate how refinement varied with each of the four parameters in the tournament. For this section, and much of the following two, I used two straightforward measures of refinement. The first is the proportion of REFINE moves averaged over each simulation (i.e. over both strategies for Stage I, or over all top ten strategies for Stages II and III), which quantified how much effort a strategy invested in refinement, as opposed to EXPLOITING or other learning moves. The second was the maximum final refinement level (i.e. the maximum refinement level of any act at the end of the simulation), as a measure of the population-level result of this investment in refinement. The two measures were evidently linked, as a higher proportion of REFINE moves would lead to higher final refinement level. Nonetheless, given that the final refinement level is a simulation-level measure, and each simulation contains at least two strategies, which potentially use REFINE moves at different rates, the two measures capture slightly different dynamics. Here I present results from the first two stages of the tournament. Stage III included the same strategies and the same parameter values as Stage II, but showed much less variability, so it was excluded from this analysis.

In the first stage, the only parameters varied were $n_{observe}$ ={1, 5} and p_c = {0.001, 0.01, 0.1}. In the second stage, as mentioned above, we ran two sets of simulations, one where we systematically varied parameters, and one with parameters drawn from more biologically realistic distributions. The systematic parameters using in the second stage were p_c = {0.001, 0.005, 0.01, 0.05, 0.1, 0.2, 0.4}, $p_{copyFail}$ = {0, 0.01, 0.05, 0.1, 0.15, 0.25, 0.5}, $n_{observe}$ = {1, 2, 5, 10}, and r_{max} = {10, 25, 50, 100, 500, 1000}. The distributions of the random parameters were skewed toward intuitively biologically relevant levels (Fig. 2.2). For example, an environmental change rate of 0.5 means that every other round the environment changes, which is not necessarily a situation we would expect culture to have evolved in, therefore we skewed the distribution towards smaller values.

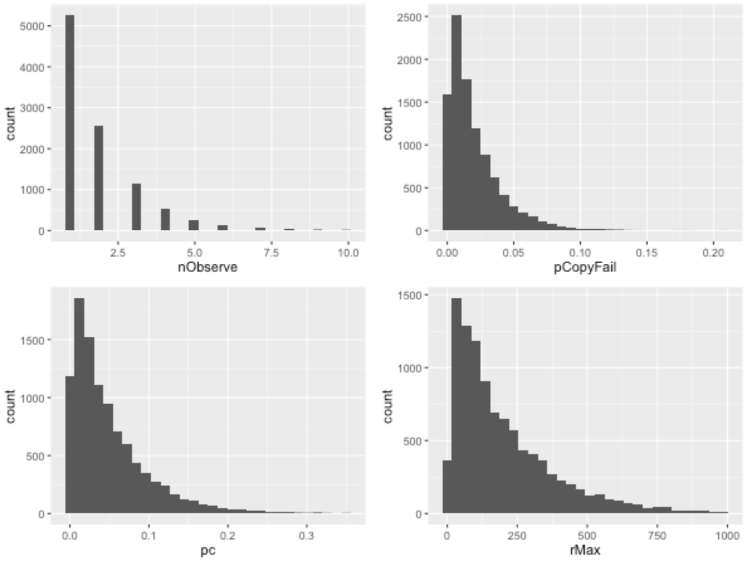


Figure 2.2 – distribution of random parameters used for Stage II

2.3.2. Results

2.3.2.1. Stage I

In the first stage, the average refinement level increased over time throughout all simulations, as expected as the population accumulates improvements, but it remained constantly higher for higher values of both $n_{observe}$ and p_c (Fig. 2.3a). Higher $n_{observe}$ meant each individual could learn from more individuals, so information spread faster in the population. This allowed agents to both learn refined moves quicker, and refine them themselves, thus leading to a generally higher level of refinement overall, compared to the case where $n_{observe}$ is 1.

A higher environmental change rate, here illustrated by higher p_c, required more learning to make sure agents have up-to-date information. This would imply more INNOVATE and OBSERVE moves, but results also show an increase in the refinement level. The advantage of refinement is that it allows the population to overcome environmental variability by investing in refining a small number of behaviours to the point where their payoffs exceed any decrease in payoff due to environmental change, but the benefit of refinement only becomes evident once the population has reached this optimally refined stage. The fact that here a higher probability of environmental change was associated with a higher refinement level suggests that strategies did indeed use refinement in order to refine themselves out of the environmental variations. As the environment changes more quickly, it pays to invest in refining out of it more than finding a good, stable payoff.

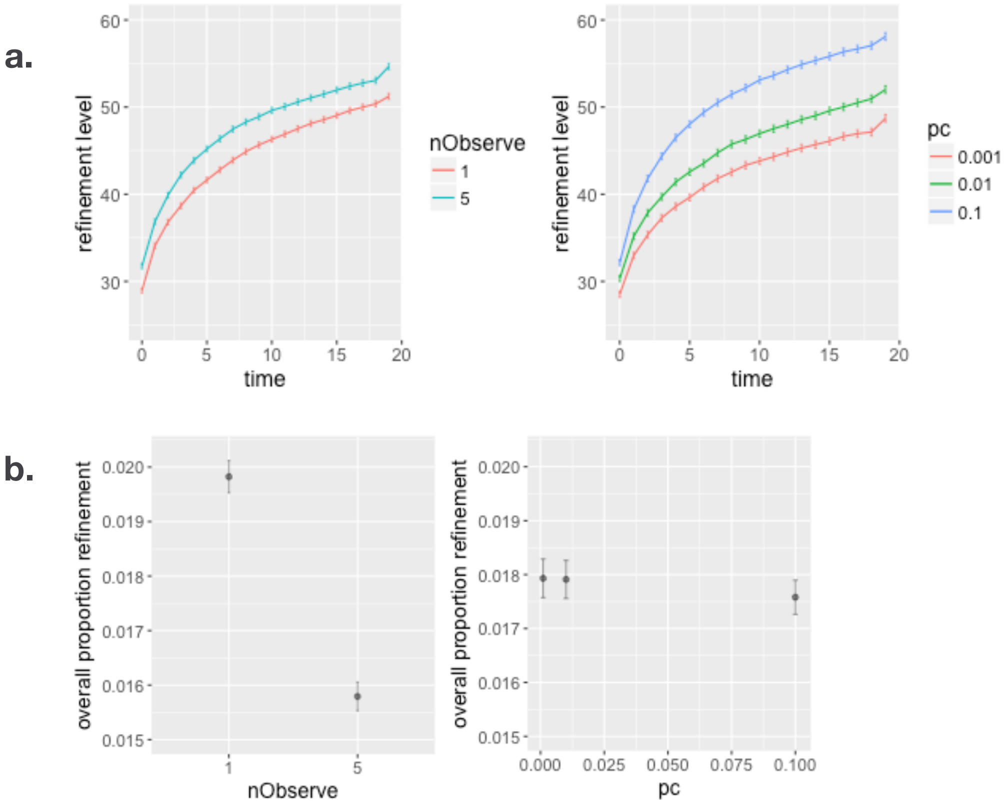


Figure 2.3 – (a) timeline of refinement level for all simulations in Stage I, by different values of $n_{observe}$ and p_c. Maximum refinement level values calculated for each simulation every 500 iterations, and averaged over all simulations in each parameter value. (b) proportion of refine moves averaged over all simulations, for the same parameters. Values were plotted on the same scale for ease of comparison. Standard error bars are included for all measurements

The proportion of refine moves paints a picture in line with these conclusions (Fig. 2.3b). The proportion of REFINE moves was lower when $n_{observe}$ was 5, presumably because as the information spread faster in the population, agents did not need to invest as much time in refinement. On the other hand, in this case the proportion of REFINE moves did not change significantly across p_c value, although we saw clear differences in the refinement level (Fig. 2.3a). This is a puzzling result and most likely due to the large variation in strategies competing in the first stage, which might be using refinement sub-optimally such that on average there is no difference in the proportion of REFINE moves, but the better strategies successfully increase refinement level overall. This question is fully explored in the next section presenting results from the second stage, which included only the best performing strategies and varied p_c values more widely.

2.3.2.2. Stage II

The second stage included only the best scoring 10 strategies, but a wider range of parameter values. It is worth pointing out, before I present the refinement results, that the broader parameter space did not change the ranking significantly. With two exceptions in strategies in the lower end of the ranking, the rankings of the top ten strategies remained unchanged across all four parameters we varied. We did see a larger distance between the scores of the top 3 or 4 strategies and the rest at higher values of p_c, $p_{copyFail}$, and $n_{observe}$, indicating that the best strategies were perhaps better at handling 'tougher' conditions. R_{max} showed no effect whatsoever on the rankings or the differences in score between strategies. Overall, the better strategies were consistently better across the whole parameter range.

The proportion of REFINE moves used varied systematically with all of the parameters (Fig. 2.4b). As in the first stage, a higher $n_{observe}$ was associated with fewer REFINE moves, since the information spread more quickly though the population. Similarly, higher p_c values meant more REFINE moves, because rapid changes prompted increased investment in refinement as agents needed to find (or, in this case, craft) more rewarding acts when the environment changed more quickly. In addition, the proportion of REFINE moves increased with higher $p_{copyFail}$. A higher probability that an OBSERVE moves fails means agents need to find alternative means of acquiring beneficial acts, refinement being one of them.

Finally, higher r_{max} was also associated with a higher proportion of refinement, as r_{max} was essentially a cap on how high a refinement level the population can achieve, and how valuable refinement is overall. This effect was a great deal smaller than it was the case with the other three parameters

(Fig. 2.4b for comparison), and the differences decrease for higher values of r_{max}.

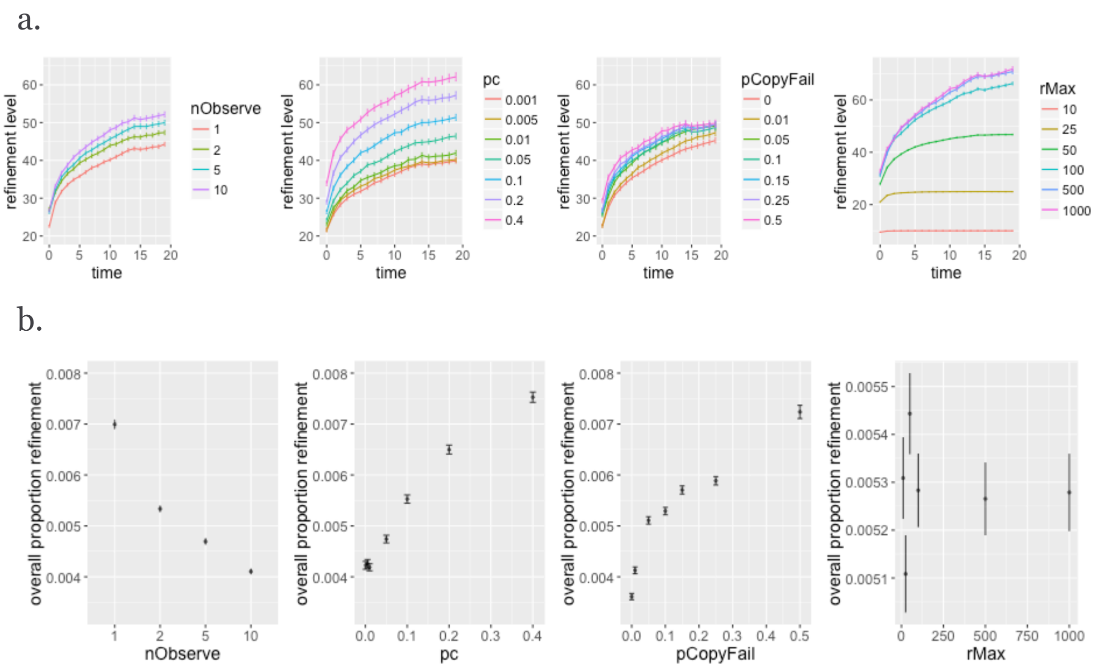


Figure 2.4 – **(a) timeline of maximum refinement level for all the simulations in Stage II for different values of the four parameters explored – $n_{observe}$, r_{max}, $p_{copyFail}$, and p_c; (b) overall proportion of REFINE moves averaged over all simulations in Stage II as a function of the four parameters. Standard error bars are included for all measurements. Results from the systematic parameter simulations**

The timelines of the refinement level are in line with both the results from Stage I, and what we would expect having seen how the proportion of REFINE changed across parameters (Fig. 2.4a). Once again, higher p_c and $p_{copyFail}$ were both associated with higher refinement levels, due to the higher proportion of REFINE moves they promote. A higher number of models was associated with higher refinement levels, despite requiring a smaller proportion of REFINE moves, as the information spread more quickly when a higher number of models was available.

R_{max} affected the value of refinement, as we saw in the previous section, but a smart refiner should not be influenced by r_{max} as much when the improvements from additional refinements begin to drop off (i.e. r_{max} over 100-200). Indeed, as the timeline graphs indicate, lower values of r_{max} limit both the highest refinement level that can be achieved, and how long it takes to achieve that maximum level. Once r_{max} exceeded 100, though, there seemed to be little difference in the trajectory of the curve, and the increase in refinement did not differ quantitatively or qualitatively. Very similar patterns were seen in the random parameter space exploration, but slightly complicated by the noisier results in the less biologically plausible areas that were less explored because of the skewed distributions.

2.3.2.3. Over-refining and r_{max} in Stage II

There was an interesting relationship between the r_{max} values explored and the maximum refinement level at the end of the simulation, caused by how the diminishing returns curve characterising the refinement increment affected how strategies use refinement. Investing in increasing the refinement level becomes less beneficial once the refinement level reaches a value around 100, as the increment becomes to plateau (Fig. 2.5a). Strategies conspicuously recognised this as the final refinement level patterns looked very different for different values of r_{max} (Fig. 2.5b).

For r_{max} values under 100, the final refinement level was highly left skewed, suggesting that strategies over-refined. This over-refinement is most plausibly due to the fact that strategies were attempting to achieve the optimal refinement level where the increment plateaus and refinement stops paying off. When r_{max} was allowed to exceed 100 (i.e. r_{max} = 500 and 1000), refinement levels were distributed efficiently with a mode at the optimal refinement level. Although there is variation in where the different simulations set the threshold of when refinement stops being useful, none of them mindlessly continue over-refining. This over-refining phenomenon also explains why there was no difference in the dynamics of refinement level over time for high values of r_{max} in the previous section (Fig. 2.4a) – once r_{max} was allowed to go over 100, strategies used refinement rationally.

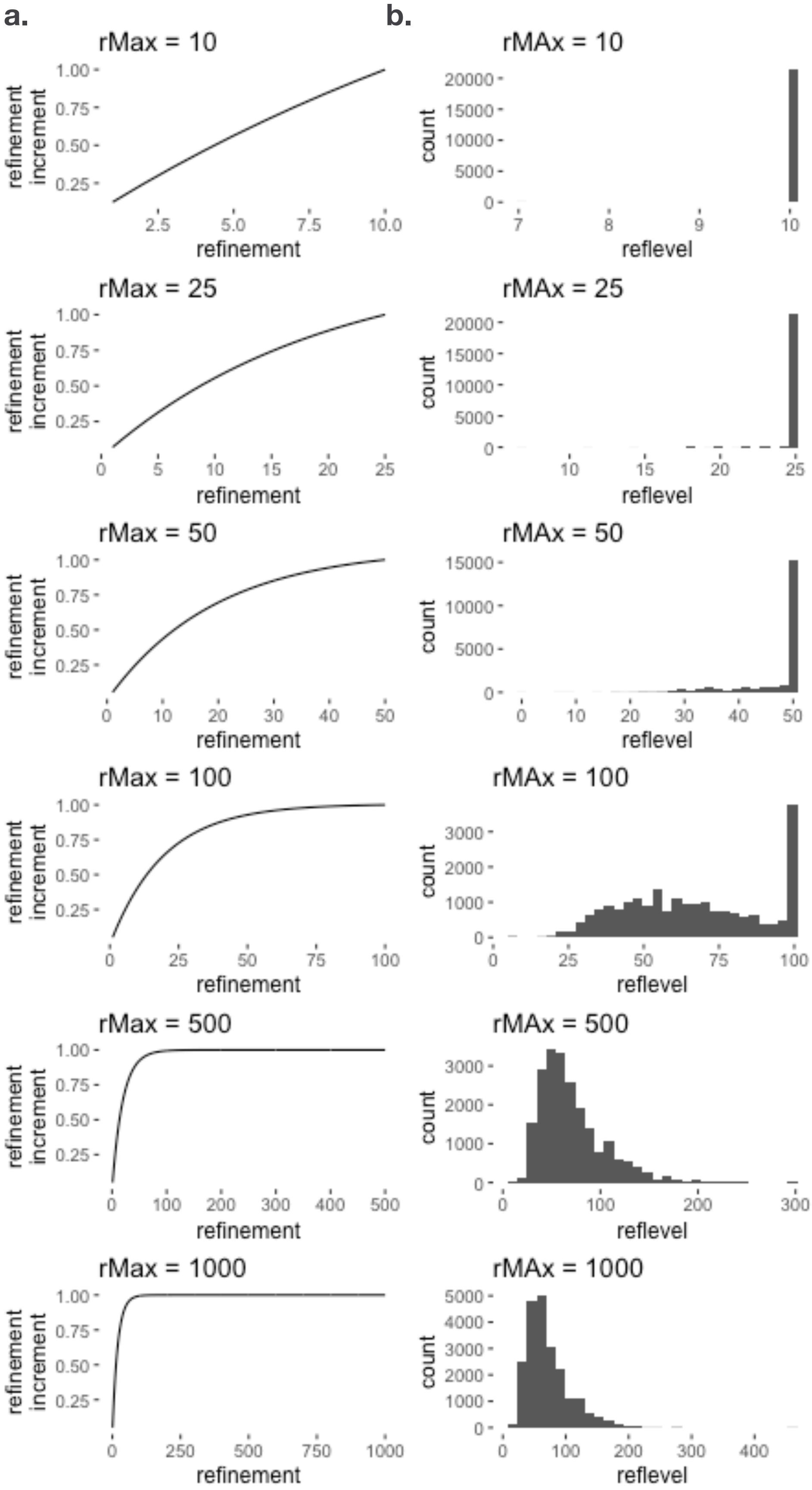


Figure 2.5 – (a) relationship between r_{max} and refinement increment as defined by the increment function in Equation 1 and (b) final maxmimum refinement level distribution for all simulations in Stage II, grouped by r_{max}

2.4. How much refinement occurred?

2.4.1. Methods

This analysis focuses on how strategies used refinement and uses data from Stage I of the tournament because it displayed the most variation in terms of strategies. In this stage all 51 competing strategies were present and competed pairwise, while the following stages only focused on the subset of strategies that have performed the best in Stage I. Therefore, Stages II and III only consisted of well-performing strategies, and will be the focus of following sections. However, since I was interested in characterising general behaviour in terms of refinement in the tournament, the analysis incorporated the full set of strategies, which varied both in performance and their use of refinement.

I initially investigated whether refinement was beneficial to a strategy's score by examining the relationship between score and the proportion of each move available. For each strategy I averaged the score (i.e. frequency of the strategy at the end of the simulation) that the strategy achieved across all the simulations it was involved in as part of Stage I. Similarly, I averaged the proportion of each of the four available moves used over all the simulations that strategy was part of. This results in an average measure of performance for each strategy, as well as an average measure of how much each strategy made use of each of the four available moves.

To further establish whether refinement was beneficial at the strategy level, I investigated whether there was a difference in performance between strategies that used REFINE moves and strategies that never did. Because REFINE moves have a profound effect on the environment by increasing the overall refinement level and thus affecting the inherent value of refinement, I also investigated whether this difference in performance between strategies that did or did not make use of REFINE moves depended on the interaction between strategy type and the type of refinement environment (i.e. how refined the environment is).

For this purpose I used average strategy-level measures. I categorised strategies as either using REFINE if the strategy ever made use of a REFINE move in any simulation, or non-refine if it never did. Similarly, I categorised the environment as either fully-refined if the final refinement level at the end of the simulation was the maximum possible value, 100, or non-refined if that was not the case. For each strategy I calculated two average scores – one was the average score of the strategy in all the simulations that were classified as a refined environment, and one was the average score of the strategy in all the simulations that were not a refined environment. Thus our sample includes 102 scores – each of the 51 strategies in each of the 2 possible refinement environment types.

I used non-parametric Wilcoxon signed-rank tests to establish whether the differences in score between the two types of strategies were significant. I used the same test to establish whether scores in different refinement environments were significantly different. In order to investigate the interaction between the type of refinement environment and whether a strategy used REFINE moves or not, I fitted a linear model using strategy score in either type of environment as a dependent variable, and environment type, strategy type, and their interaction, as explanatory variables (Equation 2.2). The model included average score per strategy (the average score of a strategy in all simulations, irrespective of environment) as an offset, to control for the fact that some strategies may be inherently better in the tournament, regardless of their approach to refinement.

$$score_i = \beta + Offset + \beta_1 Environment_i + \beta_2 Startegy_i + \beta_3 Environment_i Strategy_i + \varepsilon_i$$

$$\varepsilon_i \sim N(0, \sigma)$$

(Equation 2.2)

2.4.2. Learning and refinement

Firstly, the strategic nature of the task impacts how much time individuals should spend learning or exploiting. Given that the only way to accumulate payoff was to exploit, but individuals needed to make sure they were exploiting the behaviours that were most in line with the current environment to reap the highest payoff, there was a trade-off between learning and exploiting. A smart agent should learn as little as possible in order to make the most of exploit moves, while still using an efficient learning algorithm that allows them to acquire the best behaviours. This trade-off was reflected in the proportion of moves in use in the tournament (Fig. 2.6). EXPLOIT was overwhelmingly more common, followed by OBSERVE, with INNOVATE and REFINE moves being quite rare.

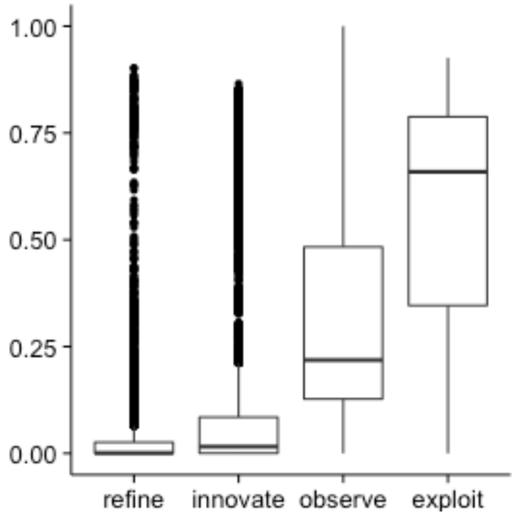


Figure 2.6 – overall proportion of moves for all 51 strategies in the tournament

The relationship between the proportion of each move and score indicates that strategies that were better at managing this learning/exploiting trade-off were more successful in the tournament (Fig. 2.7). There was a significant positive relationship between score and the proportion of EXPLOIT moves (Spearman's rank correlation $\rho = 0.82$, $p < 0.001$), while all the learning moves were negatively correlated to score. The relationship between the score and the proportion of OBSERVE moves was significantly negative (Spearman $\rho = -0.45$, $p < 0.001$), and so was the relationship between score and the proportion of INNOVATE ($\rho = -0.68$, $p < 0.001$, excluding strategies that never innovate) and REFINE moves ($\rho = -0.397$, $p = 0.019$, excluding strategies that never refine). This again reiterates the point that learning too much is costly.

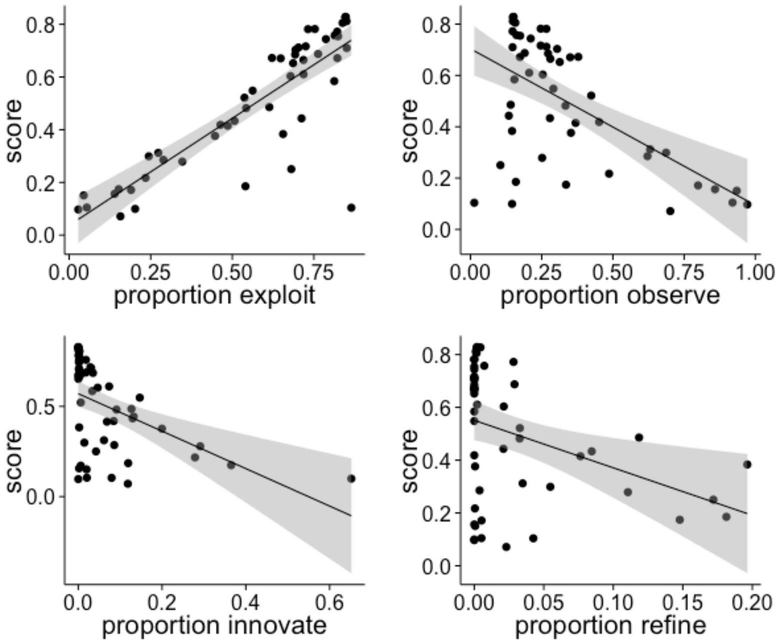


Figure 2.7 – Relationship between score and the proportions of EXPLOIT, OBSERVE, INNOVATE and REFINE moves, averaged over each strategy

With regards to learning, results confirmed the general conclusion from the first tournament – copying paid off. There was a positive relationship between the proportion of learning moves that are OBSERVE and score, suggesting that social learning is beneficial (Fig. 2.8).

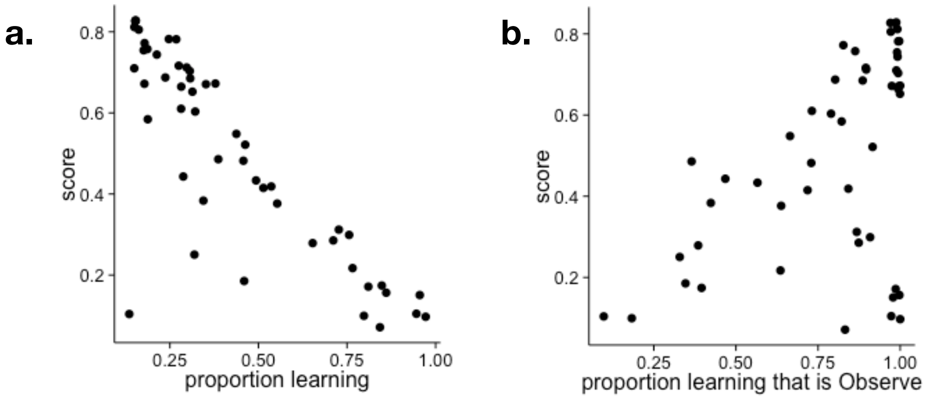


Figure 2.8 – (a) relationship between score and proportion of learning moves and (b) proportion of learning that is OBSERVE, averaged over each strategy

On the other hand, the proportion of REFINE moves did not seem to have that large of an effect on performance (Fig. 2.9a). REFINE moves are learning moves that are relatively equivalent, at least in terms of frequency, to INNOVATE moves. Therefore we would expect that if indeed there was a relationship between the amount of refinement and score, this relationship would be more evident when we excluded EXPLOIT moves that were overwhelmingly frequent, and compared REFINE with more equivalent types of moves. Nonetheless, there was no significant relationship between the proportion of REFINE moves relative to all learning moves and score (Spearman's ρ = -0.21, p = 0.21), or between the proportion of REFINE moves relative to INNOVATE moves (Spearman's ρ = 0.28, p = 0.1; Fig 2.9). This suggests that the relationship between the amount of refinement and score was not very strong, and overwhelmed by the very strong effect of how much a strategy played EXPLOIT had on its score.

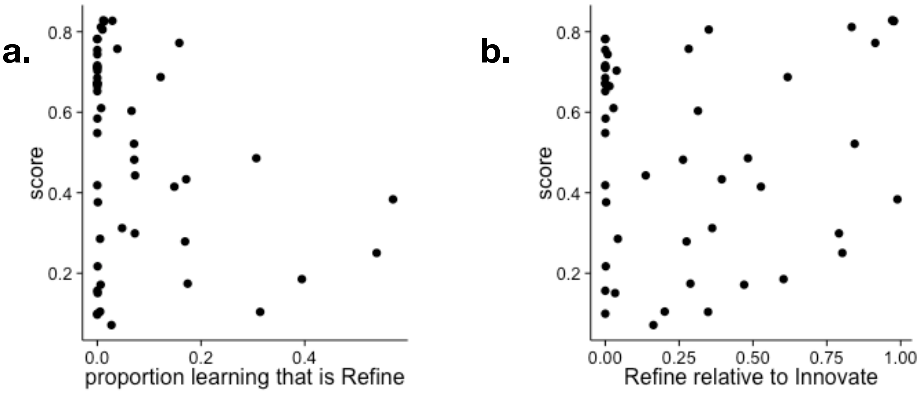


Figure 2.9 – (a) relationship between score and amount of REFINE as a proportion of all learning moves and (b) as a proportion of just REFINE and INNOVATE learning moves

2.4.3. Overall refinement

A straightforward way to quantify how much refinement was taking place in each simulation is to measure the maximum refinement level achieved by the population at the end of the simulation. In the first stage, there was a strongly bimodal distribution in the tournament results – most of the simulations exhibited either very low or very high levels of refinement (Fig. 2.10). This pattern is partly due to the fact that 15 out of the 51 entrant strategies never make use of the refine move. Excluding the strategies that do not use refine does not however change the picture qualitatively: there was still a considerable number of simulations in which the refinement level stayed very low (Fig. 2.10). This is because there was considerable variation in how strategies employ refinement moves (Fig. 2.11). Overall, 60% of the simulations achieved a final refinement level of 100, the maximum value.

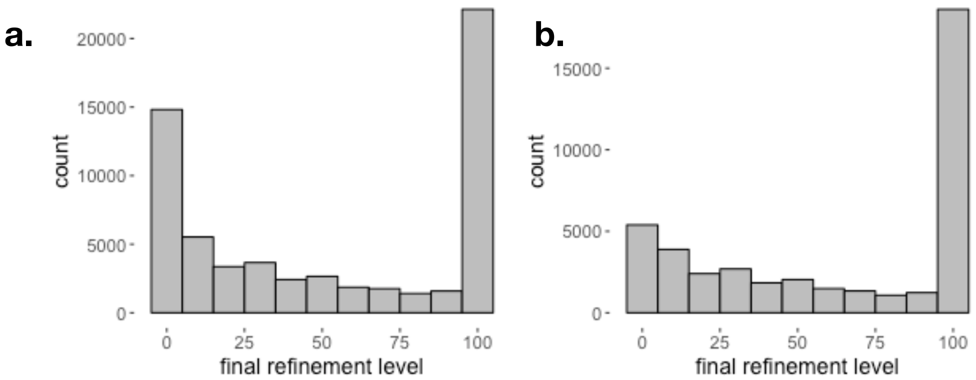


Figure 2.10 – (a) distribution of final maximum refinement level in the tournament in all simulations and (b) in simulations that include only strategies that use refine

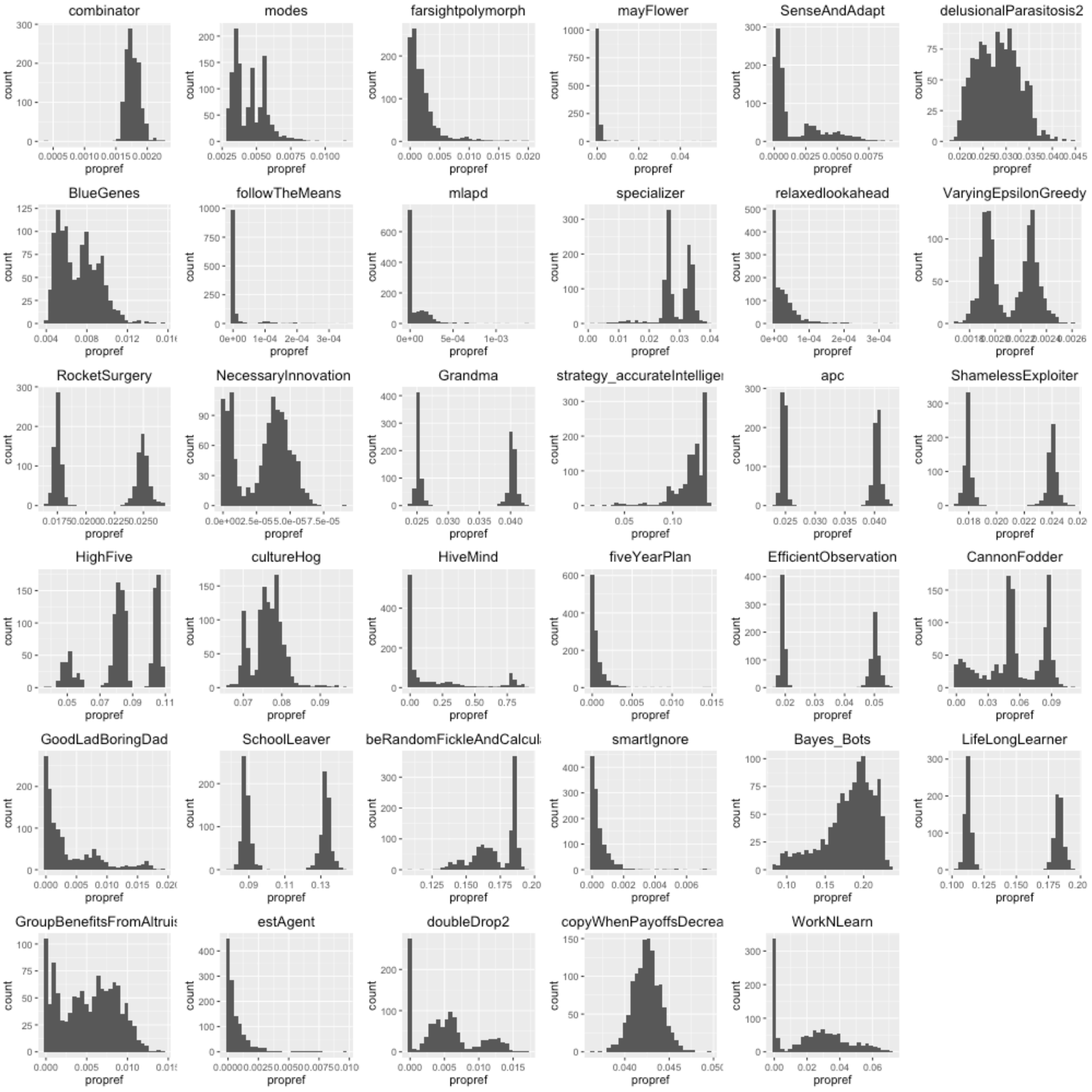


Figure 2.11 - distribution of mean proportion refine moves per simulation for each strategy, ordered from the top left by score in descending order

A refined environment should be beneficial irrespective of whether a strategy plays REFINE or not, because it merely ensures that some acts are disproportionately more advantageous. With respect to how beneficial it is for a strategy to use REFINE, we had no expectations. One the one hand, it could be that strategies that use REFINE, compared to strategies that do not, manage to use refinement as a niche-construction-like process to transform the environment so it becomes more advantageous for them to play in. On the other hand, refinement is costly, so it could be the case that strategies that use REFINE actually lose out by investing moves in refinement, while strategies that do not benefit from the extra EXPLOIT moves.

However, there was no significant difference in score between strategies that did and did not use REFINE moves (W(102) = 1382, p = 0.059) and, if anything, there was a trend towards non-refine strategies performing better (Fig. 2.12 – although the difference in performance between the two types of strategies was not significant when comparing average scores, it was actually significant when comparing the full distribution of scores in all simulations – W(61200) = 451 x 10^6, $p < 0.001$). It seems that a strategy can do well in an environment that allows for refinement even if it does not use refinement itself.

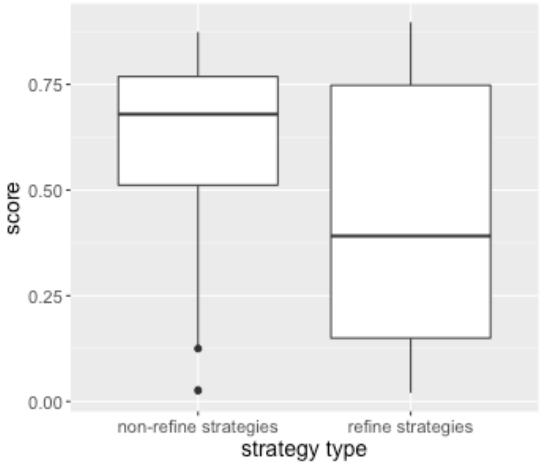


Figure 2.12 – average scores for strategies that never use REFINE moves (left), and strategies that do (right), respectively

2.4.4. Refinement environments

The divergent distribution in the amount of refinement that takes place across simulations was unexpected. As mentioned above, a refined environment should be beneficial for all strategies, irrespective of whether they use REFINE or not, but given that there was a difference in performance between strategy types, perhaps strategies behave differently in a fully refined environment as opposed to a non-refined environment. There was a significant difference in average scores between strategies that found themselves in a fully refined environment and the strategies that found themselves in a non-refined environment (Wilcoxon $W(102) = 947$, $p = 0.018$), with scores in a fully refined environment being significantly higher than scores in a non-refined environment (Fig. 2.13).

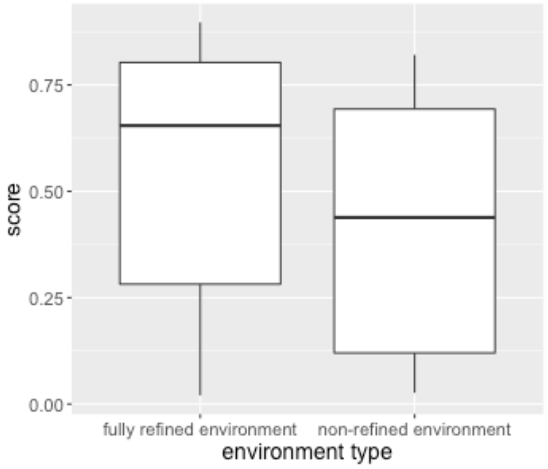


Figure 2.13 – average scores for all strategies in different refinement environments: fully refined (left) and unrefined (right)

Interestingly, average scores showed a different distribution depending on the refinement environment to which they belonged (Fig. 2.14). While scores in a fully refined environment were skewed towards higher values, scores in the non-refined environment exhibited again an abrupt split, with most values clustering at extreme values.

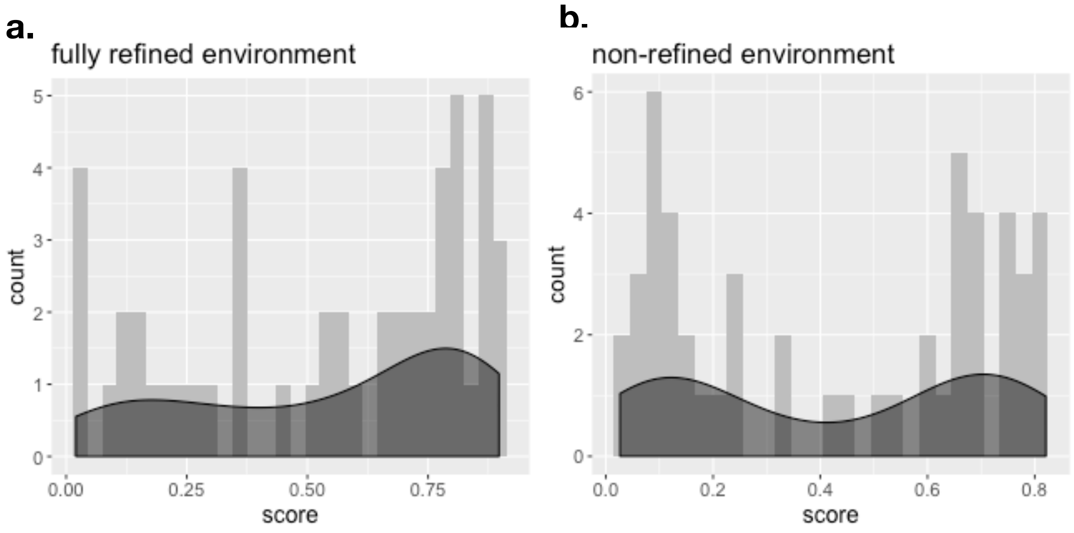


Figure 2.14 – (a) average score distributions and density plots in a fully refined environment and (b) a non-refined environment

Breaking this down further, there was a difference between the performance of strategies that used REFINE moves and strategies that did not in different refinement environments (Fig. 2.15). It seems that strategies that did not use refine were unaffected by the type of refinement environment they found themselves in, while strategies that made use of refine were highly sensitive to the environment, performing worse in a non- refined environment but also modifying their environment through refining into one in which they do better.

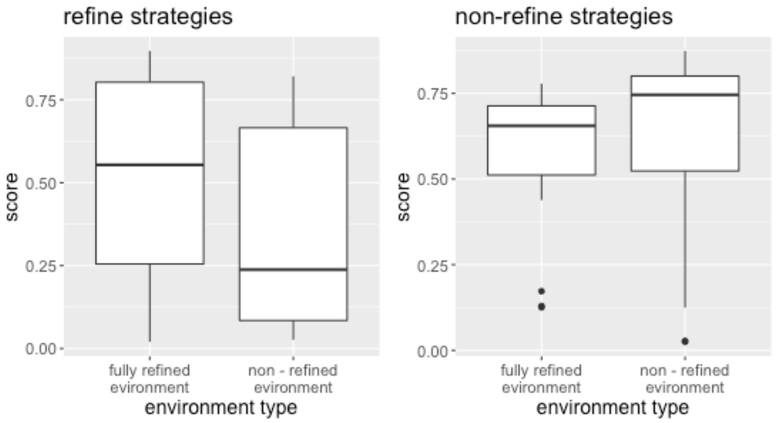


Figure 2.15 – average score distributions for by environment type, for both strategies that do and do not use refine

Results from the linear model described in the Methods used in order to investigate the interaction between the type of refinement environment and the type of refine strategy are shown below in Table 1, and assume a non-refine strategy in a non-refined environment as the baseline. Since the model included the average score for each strategy as an offset, the results represent an average increase or decrease in score relative to this average score depending on the strategy type and the refinement environment type. The model confirmed the interaction, and was notably powerful in explaining score variation - the model explained 80% of the variation (adjusted R-squared = 0.809, F(3,98) = 144.3, p < 0.001).

Variable	β coefficient	Standard error	t-value	p-value
Intercept	**-0.0008**	**0.0315**	**-0.026**	**0.97**
environment type:refined	**0.0306**	**0.044**	**0.686**	**0.49**
strategy type:refine	**-0.108**	**0.038**	**-2.856**	**0.005 ****
Environment:refined * strategy:refine	**0.131**	**0.053**	**2.441**	**0.016 ***

Table 2.1 – results from the linear model score ~ environment*strategy + average_score

The results indicate that the type of environment in terms of refinement was not a significant predictor of score, but whether the strategy usesd REFINE was, and so was the interaction between environment type and strategy type. This interaction was driven by the strategies that used REFINE, which showed a large difference in score depending on the environment type they found themselves in (Fig. 2.16). Strategies that refine performed significantly better in a refined environment, but the type of environment did not seem to matter for strategies that did not use refine. Indeed, this model confirms that a mismatch in environment and strategy types is not beneficial for either strategy type, but refine strategies are particularly affected. For a refine strategy, it is plainly beneficial to be in a refined environment.

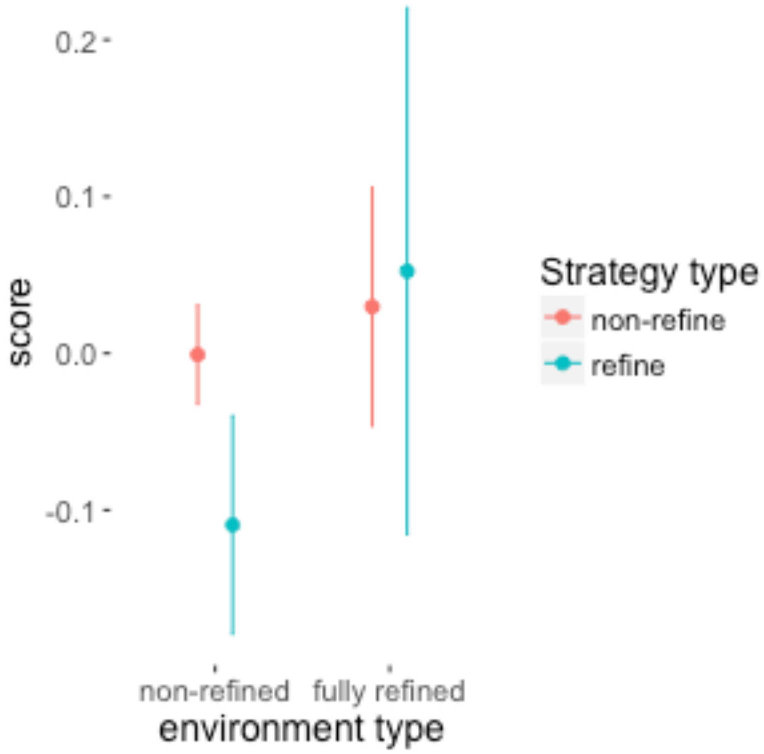


Figure 2.16 – Predictions from the linear model score ~ environment*strategy + average_score presented in Table 1. The points plot the average increase or decrease relative to the average score, and the bars indicate standard errors

2.4.5. Discussion

Naturally, the refinement environment a strategy finds itself in is not imposed top-down, but is the result of an interaction between the refinement moves performed by the two strategies competing in each pairwise Stage I simulation. Therefore, this result that refine strategies do well in a refined environment could mean that in fact, successful refine strategies are good at transforming the environment into a refined environment, while good non-refine strategies are good at ensuring the environment is not refined, potentially by invading the other strategy before it has time to achieve high refinement levels. Therefore, a refine strategy that finds itself at the end of the simulation in an unrefined environment was probably not very successful at invading and ensuring full refinement – similarly, a non-refine strategy that finds itself in a fully refined environment was probably taken over by a refine strategy. A fully refined environment should be beneficial to any strategy, as long as they implement a learning algorithm that is successful enough to take advantage of this benefit. The conundrum posed by refine strategies not performing well in a refined environment could have an easy explanation – not all refine strategies make use of an efficient learning algorithm, and therefore do not manage to take advantage of the refined environment nor prosper during that period before high levels of refinement are achieved.

The relationship between score and final refinement level suggests this was indeed the case (Fig. 2.17). There was a significant negative correlation in the case of non-refiners (Spearman ρ = -0.78, p<0.001), suggesting that good non-refiners were good at invading quickly, before the other strategy has time to refine. When non-refiners lose out to refining strategies, then the latter also ensure a refined environment, creating this negative relationship. On the other hand, there was no relationship in the case of refiners – there were plenty of refiner strategies that performed well at all average levels of refinement. This was caused by a complicated relationship between refining, over-refining, and learning.

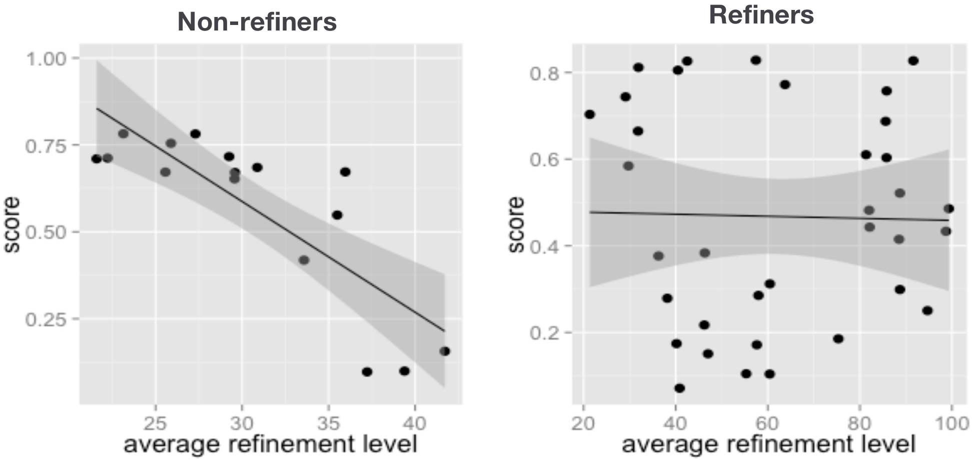


Figure 2.17 - Correlation between score and average refinement level at the end of the simulation, averaged over every strategy, for strategies that do not use refine and strategies that do use refine

When it comes to refiners playing against non-refiners, refining strategies pay the cost of lost exploit moves, but improve the cultural environment for those free-loading non-refiners. To estimate whether a behaviour is refined enough, an individual needs to refine further in order to receive payoff information, thus adding to the excess refinement. Therefore, refining above optimal levels is not a completely irrational behaviour (since some ‘test’ REFINE moves are needed to be sure that there are not further unrealised benefits available from additional refinement). It could be then that what contributes most to a refiner’s success is not how much refinement they do, but rather how good the strategy is at learning in general, and how good it is at exploiting a refined environment.

Several strategies refined more than necessary. The refinement context creates a dilemma – individuals are born in a world where refinement is beneficial, as it increases payoff, but investing moves in refining is not. Ideally, someone else would have refined already, and individuals would just have to copy those refined moves. Improving on hundreds of previous refine moves would be impossible in one agent lifespan, while copying them is cheap. Therefore the population as a whole benefits from a level of refinement much higher than what an individual benefits from. This happens because individuals benefit from being born in an already refined world where they can copy a highly refined behaviour, but do not benefit from actually investing in that refinement.

2.5. How does refinement affect cultural diversity?

2.5.1. Methods

Following Rendell et al. (2011), this section addresses the effect of refinement on cultural diversity. In this context, cultural diversity is quantified in terms of the number of acts present in the combined repertoires or expressed behaviours of all the agents the population at a specific time point (expressed as a proportion of the 100 total possible to obtain). For example, if different agents use a variety of different acts, the culture of that population can be described as relatively diverse, while a situation of low cultural diversity would be defined by a large number of agents using the same acts. This analysis entails a shift of emphasis from the individual or strategy level to population level outcomes. To measure diversity, I made a distinction between the acts the population knows and the acts the population uses. Therefore I defined 'Knowledge' as the combined repertoire of all the agents alive in the population at a certain time point, while 'Behaviour' was the set of acts being exploited in the population at that point in time.

For both, cultural diversity was quantified using metrics I terms 'amount', 'evenness' and 'persistence' (after Rendell et al. 2011). Amount was calculated as the mean or median proportion of possible acts used or known by at least one agent in each round in the last quarter of the simulations, averaged over demes in spatial extension. Evenness, the flatness of the frequency distribution of behaviour patterns across the population, was measured using Pielou's evenness index,

$$J = \frac{-\sum_{i=1}^{S} p_i \ln p_i}{\ln(S)}$$

(Equation 2.3)

Here p_i traditionally represents the proportion of species i and S is the number of species (Smith and Wilson, 1996). In the tournament context, each species i represented an act, so p_i was calculated as the proportion of agents using act i. Here maximum evenness was achieved when all possible acts are performed with equal frequency, whilst minimum evenness would represent the situation in which all agents perform the same single act. Persistence refers to the mean, median, or maximum number of rounds that an act was exploited or that knowledge of it persisted within the population, without a break, within a population. In the cumulative extension, refinement level was not differentiated – an act was treated as the same after it had been refined. We averaged each diversity measure over all simulations in a given extension, at every 1000 time steps, to see how the measure changes over time.

In the section that follows I first present basic results from the first stage, which hold for the rest of the tournament as well, and then proceed by introducing evidence from the later stages. I conclude by exploring the relationship between diversity and performance, with evidence focusing on the top ten strategies, to understand the role that refinement specifically played in the observed patterns.

2.5.2. Stage I

2.5.2.1. Cumulative extension results

I have shown above that refinement takes place, but this section will provide evidence that the presence of refinement also considerably affected the diversity of culture. The first piece of evidence for this is the observation that, as the refinement level increased, the cultural diversity decreased. Refinement level increased over time as the population gradually improved on behaviours it already knows and this lead to a decrease in cultural diversity as effective learners gradually found the highly refined behaviours and used them consistently, making them even more likely to be copied, and so forth, until all the population has focused exclusively on the single most refined behaviour (Fig. 2.18).

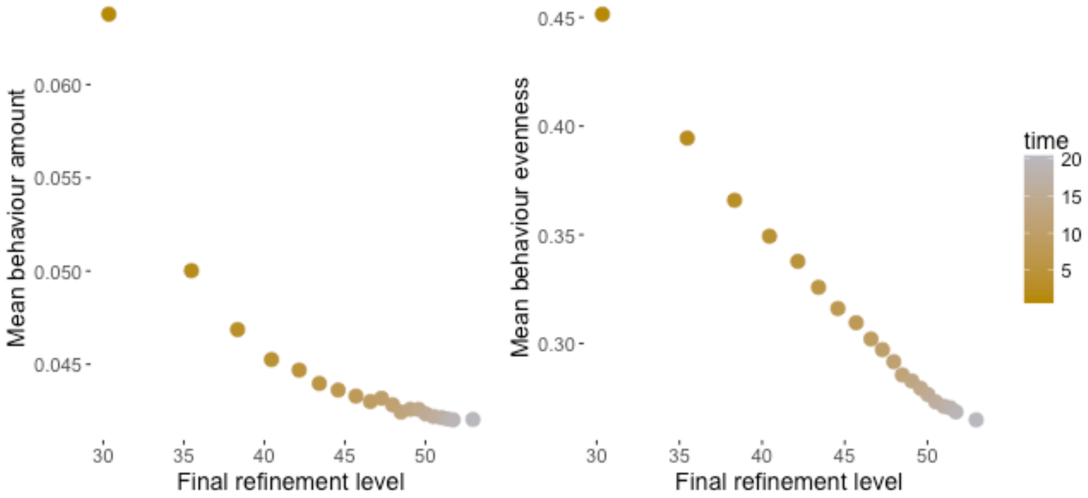


Figure 2.18 - behaviour amount and evenness as a function of refinement level over time. Each point here is an average of all simulations, taken every 500 iterations, with time indicated by symbol shading

Importantly, the population knew a great deal more than it was using (Fig. 2.19). The amount of both behaviour and knowledge decreased over time, which is not unexpected as the population is filtering and ultimately discarding ineffective acts, yet behaviour remained consistently much lower than knowledge. Crucially, the population converged very quickly on a very small number of acts. The amount values suggest that the population was using only 3-4 acts at any time, although it had around 40 in its combined knowledge repertoire.

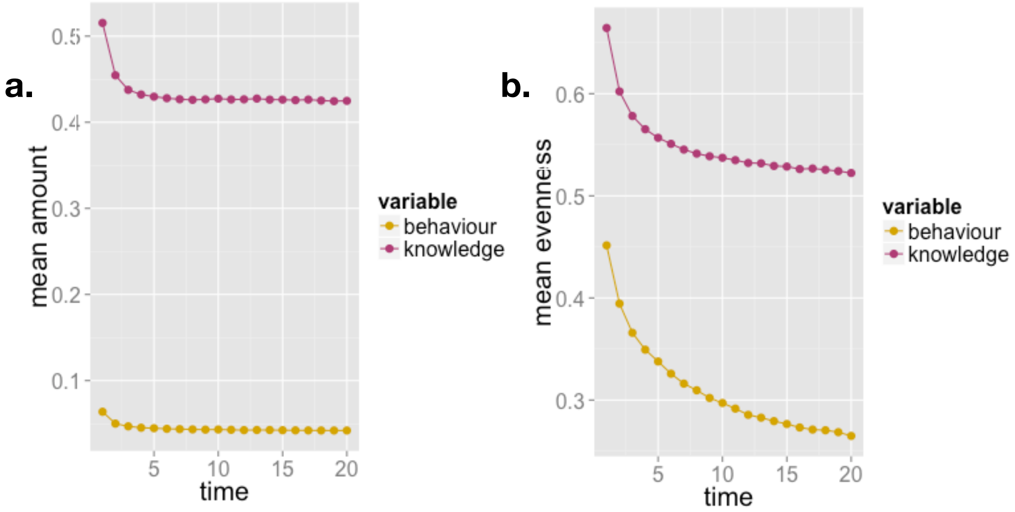


Figure 2.19 – (a) behaviour and knowledge amount and (b) behaviour and knowledge evenness as a function of time, averaged across all simulations, every 500 iterations.

A low evenness means most individuals know or use the same behaviour. When the population converges on the same acts, either in knowledge or behaviour, then evenness decreases. Therefore, here, although the population knew a more diverse repertoire, it used a very small number of acts, those that had been refined the most (Fig. 2.19b).

The data on persistence paint a similar picture. Knowledge persisted in the population longer than behaviour. Bear in mind that persistence was calculated as the number of rounds that acts were used or known by at least one member of the population. Most acts did not last in the population's behaviour or knowledge repertoires for long, but the ones that did last, lasted for a very, very long time – hence the large difference between the mean and maximum persistences we observed (Fig. 2.20) – the latter are close to the maximum number of possible rounds. These long lasting acts are the refined acts.

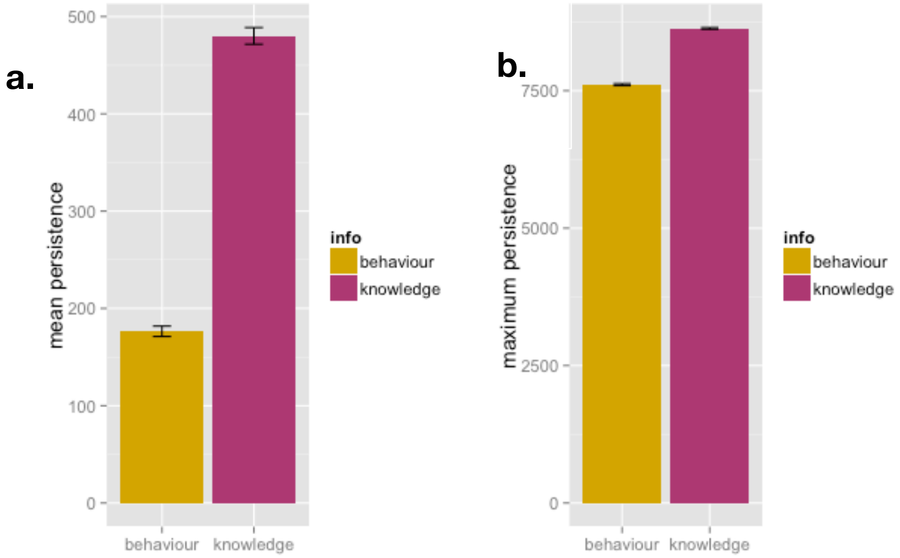


Figure 2.20 – (a) average mean and (b) maximum persistence for knowledge and behaviour

2.5.2.2. Across extensions

We can also compare cultural diversity across tournament extensions. Although I have not described results from the other two extensions in any detail, they provide control groups for understanding the effect of cumulative refinement. If the decrease in diversity described above is due to a convergence in the population on the refined behaviours, then we expect less convergence (i.e. higher diversity and evenness) in the other two extensions. Of course, convergence can occur without cumulative culture. Populations mostly containing strategies that deploy effective learning, or identify good models, would still be expected to converge on the best behaviours. Nonetheless, neither extension creates a similar situation to refinement, where the payoffs from the best behaviour are so large that environmental variation becomes proportionally negligible. In the other two extensions, even strategies that are excellent learners would still need to maintain a more varied repertoire in order to buffer environmental variation and make sure they have fall-back options in case the best act known stops being useful. Therefore, although we expect cultural diversity to decrease across all extensions, this decrease should be more dramatic in the cumulative case.

Indeed, it seems that in the absence of refinement, populations maintained higher amounts of behaviour and knowledge. This was true for both the spatial and model bias extension (Fig. 2.21), and it happened precisely because of the convergence due to refinement – individuals simply did not need to know as much as long as they had an act in their repertoire that was refined enough. Similarly, in the cumulative extension, evenness was lower, and decreased more sharply than in the other two extensions as populations homed in on the most refined behaviour and individuals ceased to learn after they have acquired it. Finally, in the cumulative extension acts persisted for longer, while the other two extensions showed considerable turnover (Fig. 2.22).

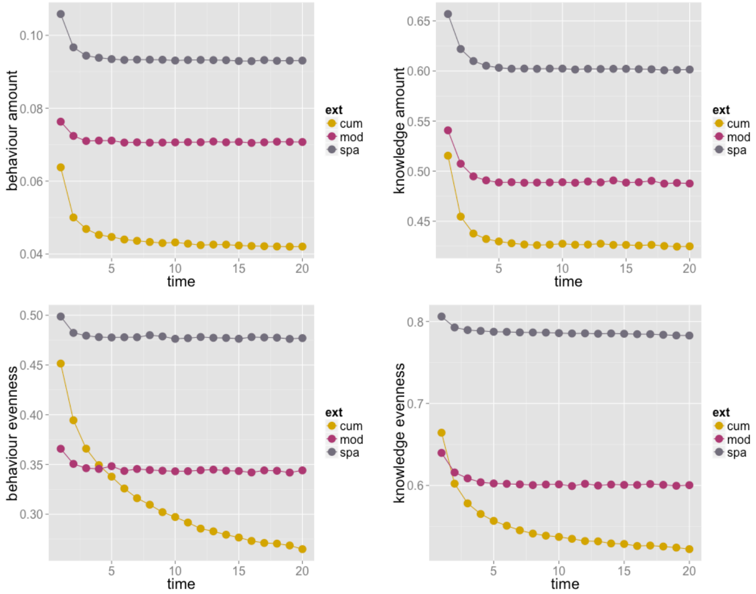


Figure 2.21 – amount and evenness for behaviour and knowledge over time, for each extension, in Stage I

Thus, in the cumulative extension behavioural diversity was lowest relative to the other extensions, decreased the most, and persisted the longest both on average and for the longest lasting act. This suggests that the population converged on a very small number of acts very quickly, and carried on using those acts for the whole time. Knowledge, on the other hand, showed a slightly more complicated pattern. The amount and evenness were, again, lowest in the cumulative case, but the persistence was lowest on average, and maximum persistence was highest. This would suggest that in the cumulative extension, the population-wide repertoire was smaller, the longest persisting acts (presumably the refined acts) persisted for a very long time, but there was higher turnover on average in the population as indicated by the average knowledge persistence, because only highly refined acts tended to get passed on by copying. The refined acts were the ones the whole population knows and uses, and therefore there was little pressure to maintain other acts in the repertoire because they would not be as useful as the refined acts, nor necessary as fall-back options. This translated into a higher turnover of acts known on average, so at any time the population repertoire consisted of very few refined acts which persisted and multiple disposable acts that the population kept replacing.

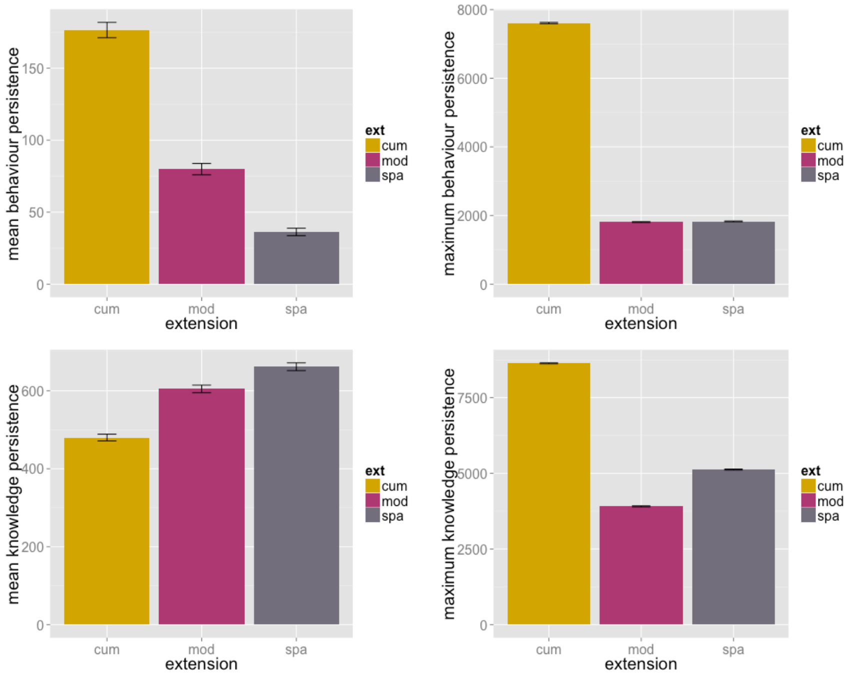


Figure 2.22 – average and maximum behaviour (top) and knowledge persistence (bottom) across the three extensions, in Stage I

2.5.3. Stages II and III

In this section I present cultural diversity results from the entire set of simulations in Stage II and III, using the full set of parameters and strategies included in each respective stage. These two stages only included the top ten performing strategies, so they provide insight into how cultural diversity changes in the context of successful strategies.

Again, the cumulative extension exhibited the most convergence, as indicated by all three cultural measures. In Stage III, with all three extensions active simultaneously, we expect refinement to have the same strong convergence effect, and consequently to drive cultural diversity in this stage to be more similar to the diversity in the cumulative extension in previous stages, and that is indeed what we found (Fig. 2.23) Population outcomes in Stage III were much closer to those of Stage II in the cumulative extension than any other extension. Even more, the Stage III results are characterised by still lower amounts and evenness of knowledge and behaviour. Likewise, maximum persistence was very high. It seems then that, in the final stage of the tournament, the cultural dynamics are most strongly influenced by the forces we see in the cumulative-only Stage II. The population is very good at converging almost immediately on a very small set of acts they continue to use for the rest of the simulation, while rapidly discarding any newly learned acts that do not prove as beneficial.

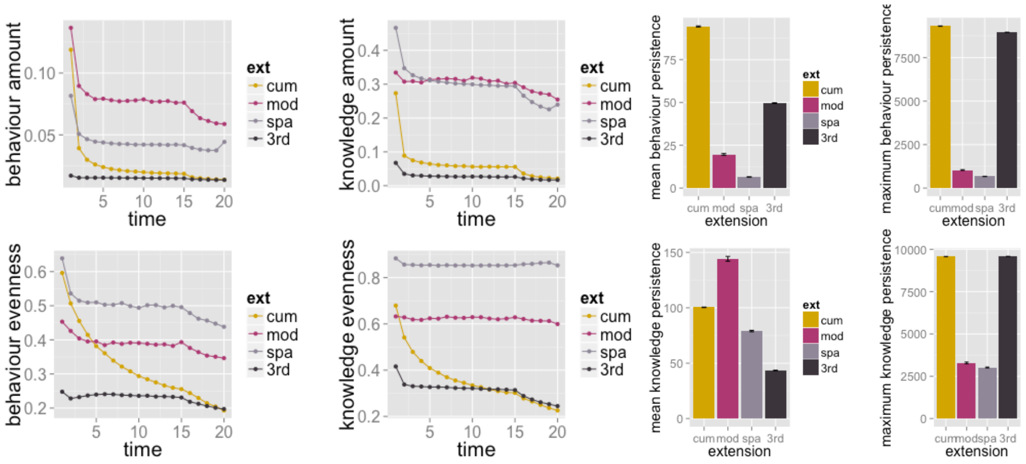


Figure 2.23 – cultural diversity measures across extension for Stage II (cumulative, model bias, and spatial extensions), and Stage III (all three extensions active, here in black). The timelines illustrate knowledge and behaviour amount and evenness over time, and the bar charts illustrate average and maximum persistence for knowledge and behaviour

2.5.4. Diversity over the parameter space in Stage II

The second stage of the tournament provides the most variation in terms of the parameter space explored, and therefore represents the focus of this section. We expected cultural diversity to vary across the parameter space, as the amount of learning and the diffusion of information changes with different parameters. When the probability of environmental change, p_c, increased, so did the amount, evenness, and maximum persistence, while average persistence lowered slightly (Fig. 2.24). These are all effects we would expect if the rate of learning increases, leading the population to maintain a larger repertoire with a higher turnover. The rate of failure of social learning $p_{copyFail}$ seems to have a similar but weaker effect on cultural diversity.

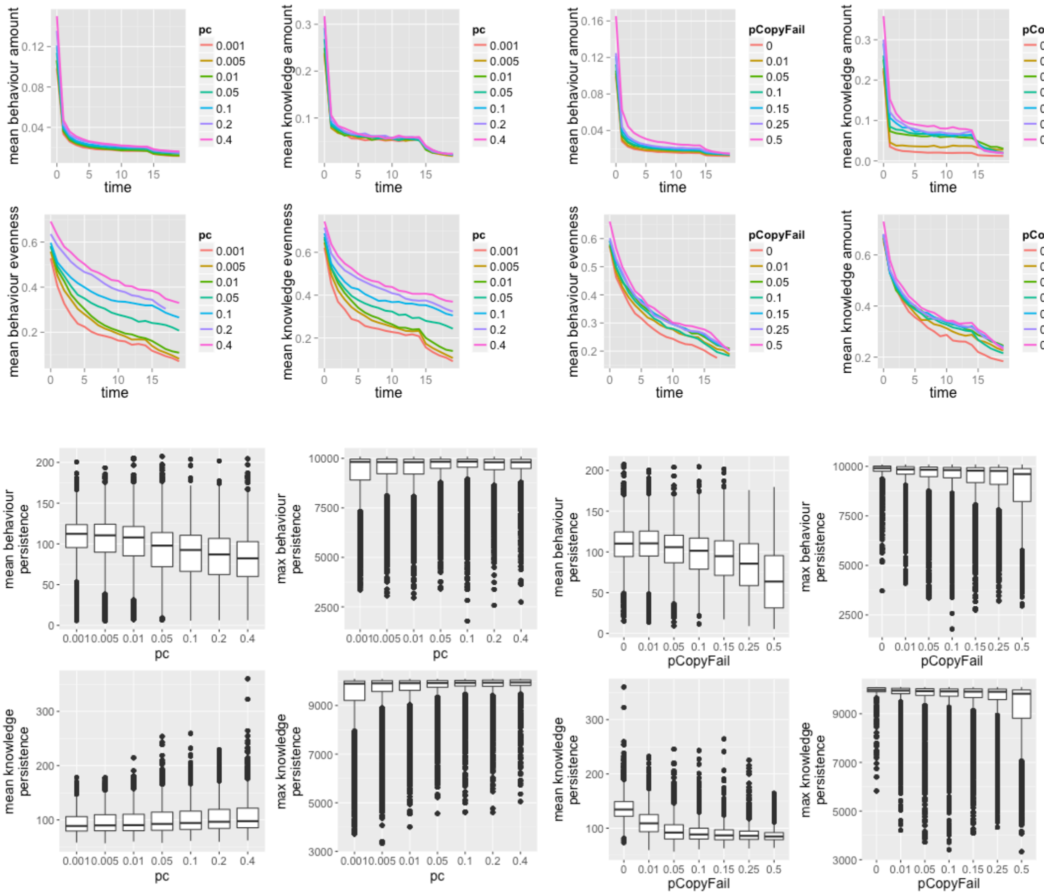


Figure 2.24 – cultural diversity measures as a function of p_c and $p_{copyFail}$ in Stage II. Timelines of amount and evenness are presented as line charts, while the boxplots illustrate mean values for mean and maximum persistence

When r_{max} increased, the amount and evenness of knowledge and behaviour decreased drastically (Fig. 2.25). Both average and maximum persistence remained relatively unchanged. Thus lower values of r_{max} were associated with lower levels of convergence. If only a little refinement is possible, then refined behaviours are not as valuable (i.e. they do not add as much increment to the basic payoff, and payoffs are still proportionally much more affected by environmental change), and individuals can themselves fully refine behaviours in their own lifetime, thus they do not need to copy many generations' worth of refinement. Therefore, there is less pressure to copy and share the refined behaviours in the population, which results in lower convergence and higher cultural diversity. Crucially, only when refinement can reach levels individuals cannot attain in their own lifespans do we see the most drastic loss of diversity.

In the case of $n_{observe}$, interesting patterns emerged from the effect the number of available models has on the diffusion of information. Both the amount of knowledge and behaviour were highest when only one model was available, but similarly lower once individuals were exposed to more than one model. Maximum and mean persistence both increased monotonically with increasing $n_{observe}$. Evenness, however, showed a different pattern. When $n_{observe}$ was 1, evenness started high and decreased abruptly. When $n_{observe}$ was high, evenness started low but did not change much. When $n_{observe} = 2$, though, the evennes started high but decreased quickly and abruptly – after a quarter of the simulation time, the evenness value was the lowest here out of all $n_{observe}$ values, and remained the lowest. Therefore this suggests we see the most drastic convergence when individuals can observe two models.

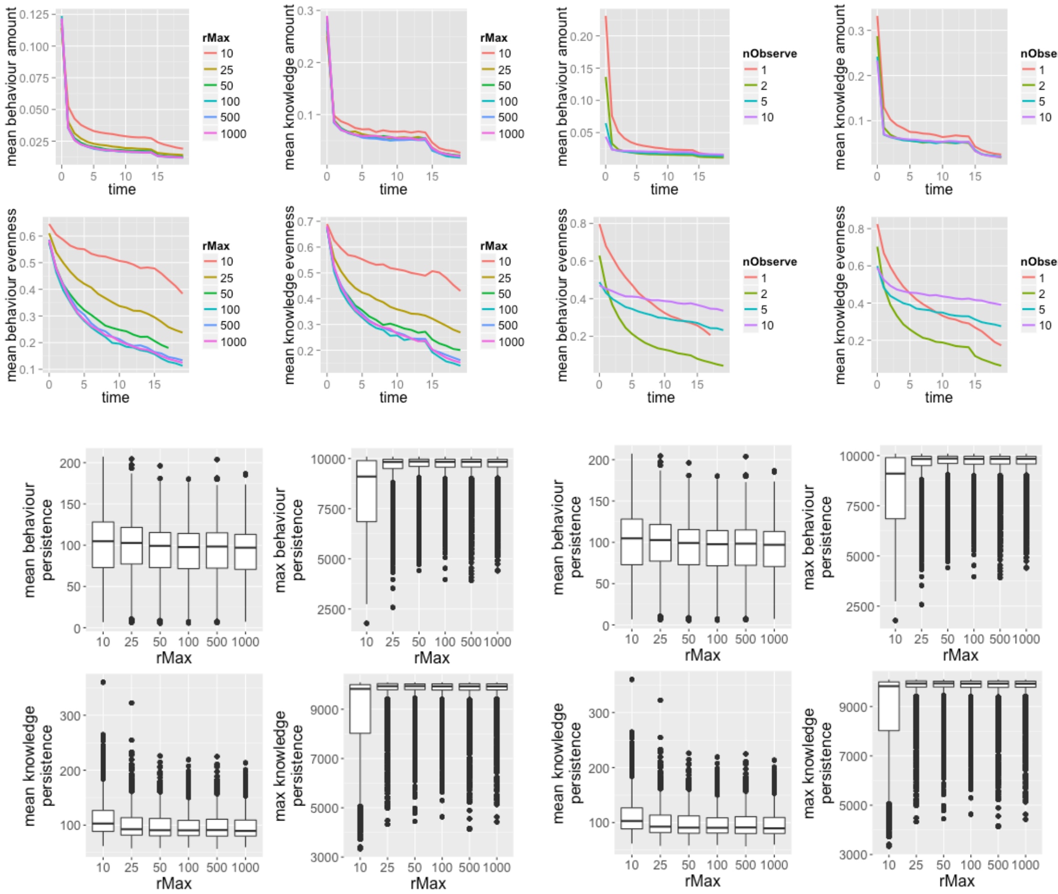


Figure 2.25 – cultural diversity measures as a function of r_{max} and $n_{Observe}$, in Stage II

The relationship between cultural diversity and $n_{observe}$ is explained by how the number of models affects the speed of diffusion, which in turn affects the rate of refinement. Assuming that in all cases agents are equally good at identifying and copying the most successful acts, they will copy the refined acts that provide the best payoff. We expect that when information spreads very fast, as is it is the case for high $n_{observe}$ values, the successfully refined acts are quickly copied and additionally refined. This would mean that at the beginning of each simulation, as information spreads quickly, there is a brief flowering of diversity, followed by quick convergence on refined acts, which persist over time. The evenness remains relatively high though, suggesting that although there is a small number of acts in the population (as the data on amount of culture illustrate), and although these few acts persist, the population converges on a more diverse set of acts which is captured by higher evnness values.

When only one model is available, information spreads relatively slowly. Individuals have a harder time identifying the best acts, which means they maintain a higher number of alternative acts in their repertoire – this is confirmed by the high amount values and low persistence. With time, though, they manage to find refined acts and converge on them, as indicated by the steady decrease in evenness. The interesting case happens when the $n_{observe}$ value is 2. Here the information spread is not too slow to inhibit quick refinement, as when $n_{observe} = 1$, but neither fast enough to allow for too much parallel refinement. It takes longer for an act to become established and refined by the population, so refining several acts at the same time is more costly. This drives the population to converge quickly on a small number of acts that persist, as confirmed by the small amount values, high persistence values, and quick and strong decrease in evenness.

2.5.5. Diversity and performance

This final section addresses the relationship between cultural diversity and strategy performance. I hypothesised that more successful strategies will be better at refining efficiently, which would translate into more drastic convergence. I isolated Stage I simulations that only included strategies that scored in the top ten, and compared them with the diversity results of simulations containing the rest of the strategies. Better learners should be able to use refinement to their advantage, and converge more effectively on the most beneficial behaviours. Therefore, I expected that the diversity measures for simulations with the top ten strategies would show higher convergence than simulations containing less effective strategies.

Indeed, the amount and evenness were lower in the best ten strategies, and acts persisted generally for a longer time (Fig. 2.26). In the case of behaviour, good strategies started with a smaller, but less even set of acts they use, as illustrated by lower amount but higher evenness values compared to the strategies not scoring in the top ten. The top ten population quickly converged on one or two behaviours, which lasted for a long time. The amount of knowledge was also very low compared to less effective strategies, with a rapidly decreasing evenness.

The longest persisting act lasted for a long time (more than 70% of the total number of rounds) in the population of top ten strategies, but the average persistence was much lower than for the rest of the strategies (Fig. 2.27). This again can be explained by convergence on refined acts. Similarly to the comparison between the cumulative extension and the other two extensions, here there is little pressure to maintain other acts in the repertoire as a backup, as long as the refined acts are known. In this case, too, we expect the top ten population repertoire would contain only a small number of refined acts that persist, along with several expendable acts that exhibit high turnover, which is what was observed. In sum, strategies that performed well in this tournament extension were highly effective at converging on highly refined behaviours.

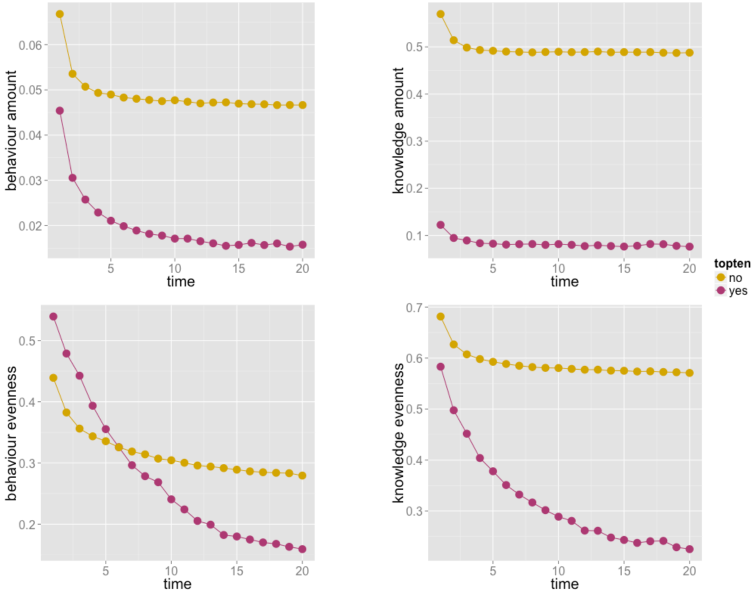


Figure 2.26 – amount and evenness, for both behaviour and amount, in simulations that only include topten strategies (pink) and simulations with the rest of the 41 strategies (yellow), in Stage I

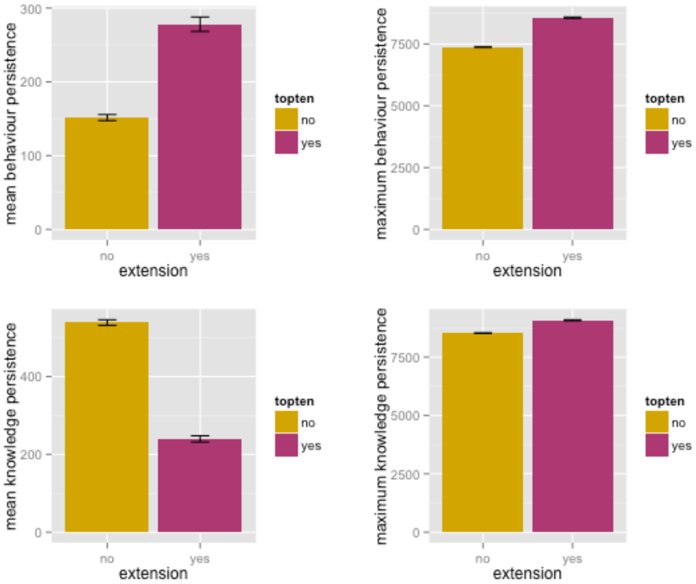


Figure 2.27 –and mean and maximum persistence, for both behaviour and amount, in simulations that only include topten strategies (pink) and simulations with the rest of the 41 strategies (yellow), in Stage I

2.6. General discussion

This chapter has shown that in the multi-armed bandit context of the tournament, playing REFINE too much is a disadvantage, like INNOVATE was in the first tournament. The trade-off between learning and exploiting means that individuals should learn as little as possible, and when learning, they should copy rather than try to individually learn or improve what they know. Therefore a rational agent should invest as little as possible in refinement, which is what the results showed.

Similarly, I found that in relation to the parameter space, refinement is employed more, like any learning move, in faster changing environments, when learning is less accurate, and when the number of models is smaller. A smaller number of available models means the information spreads slower in the population as the agents copy fewer individuals, so achieving optimal refinement levels requires a higher rate of REFINE moves. The result that a higher number of models was associated with more refinement is in line with the literature. As discussed in Chapter 1, studies using both theoretical and experimental approaches have shown that large groups promote an increase in cultural accumulation of more efficient or more complex skills (Henrich, 2004; Derex *et al.*, 2013; Muthukrishna *et al.*, 2013). This work has been mostly concerned with confirming the link between population size and cumulative culture, and less with investigating the mechanisms that might be supporting it (though see Chapter 5 for a first attempt). The number of models available for copying should surely be a relevant mechanism that, even through merely pooling a larger body of information together in a ‘collective brain’ type of effect, leads to cultural accumulation, as shown here.

When learning is less accurate, copying refined behaviours is also less reliable, which promotes an increase in refinement rates, potentially as an alternative to copying for acquiring beneficial behaviours. The fact that an increase in the fidelity of transmission can be associated with less refinement is counterintuitive in light of the literature that posits fidelity of transmission as a key factor to cumulative culture (Boyd and Richerson, 1985; Lewis and Laland, 2012; Henrich, 2016). Much work has focused on the fact that for a population to be able to improve on knowledge from previous generations, it first needs to maintain that knowledge faithfully enough from one generation to another. Therefore cultural accumulation is conceptualised as a two-step process: social learning that ensures faithful transmission, followed by individual refinement that ensures increase in efficiency. This would mean that higher fidelity of transmission should promote increased cultural accumulation, but most of this work was concerned with situations in which individual improvement in skill is not a viable alternative to copying. In this tournament that was not necessarily the case. Here refinement is beneficial, but individuals can easily invest in independently refining, so it would make sense that when copying is highly error prone, individuals would rely on refinement as a way of acquiring the best behaviours, which is what we saw.

Finally, higher environmental change was associated with more refinement, which confirms previous results indicating that cumulative culture should provide a quick and flexible way of adapting to fast-changing environments (Boyd and Richerson, 1985). In the tournament, refinement was modelled as a way of overcoming environmental variation by allowing a population to refine behaviours to such an extent that environmental variation has negligible effects on their payoffs. Therefore, if the environment changes very quickly, it is more advantageous to invest in refining rather than invest in trying to keep track of the best behaviours through either copying or individual learning. Results show that this was precisely what strategies chose to do, which resulted in higher refinement levels for higher rates of environmental change.

There is a clear strategic aspect to playing REFINE. Being in a refined population is individually beneficial, as it means one just needs to copy a well enough refined behaviour rather than invest tens of moves in trying to refine on their own. But for a population to become refined, some agents need to sacrifice moves in order to refine. This leads to a conflict of interest, since the population as a whole benefits from a rate of refinement much higher than what is individually optimal. Nonetheless, populations managed to use refinement optimally, as the observed level of refinement was consistent with values at which refinement ceases to provide increasing advantage due to the diminishing returns function associated with the refinement increment.

While non-refine strategies showed little difference in performance depending on the type of environment they found themselves in, the environment mattered a great deal to strategies that made use of refinement. By using refinement and thus overcoming environmental variation, strategies can construct a more advantageous environment through a process evocative of niche-construction (Laland, Odling-Smee and Feldman, 2000). This was clearly illustrated by the fact that strategies that used refine did not perform very well in an unrefined environment, but considerably increased in performance in a refined environment. Even more, all strategies scored better in a refined environment, indicating that indeed a refined environment was beneficial irrespective of the strategy's approach to refinement. However, there is a tension between strategies that do and do not use refine: strategies that refine pay the cost of lost exploit moves, but refine the environment for everyone. This results in non-refine strategies having a generally higher score, even if they never refine.

Cultural diversity in the simulations showed a pattern of strong convergence: the amount and evenness decreased as the population focused on a very small number of refined acts, which persisted for most of the simulation. There was sharper convergence in the cumulative extension, as expected if refinement promotes higher convergence, and in the top ten strategies, suggesting that better performing strategies used refinement more efficiently. The fact that simulations including better performing strategies are characterised by stronger convergence suggests more successful strategies are better at refining and consequently converging on the refined acts. Therefore we expect natural selection to favour strategies that perform in ways that strengthen the convergence effect, which should lead to more and more strategies that converge more strongly, which would further increase the convergence effect. It seems then that, for individuals, investing in refining is costly, while copying someone else's refinement is cheap. This leads to the entire population converging on a very small set of refined behaviours that stay unchanged. Of course, we would expect some degree of convergence in the other extensions too, as agents gradually learn the most beneficial behaviours. This effect would be stronger in the model-bias case than in the spatial extension, where having the option to choose whom to copy from facilitates effective learning and convergence on the best behaviours, and this is indeed what we saw.

Nonetheless, there seems to be a qualitative difference in convergence in the cumulative extension. More refinement of each behaviour results in higher payoff, but refinement is costly, especially the type of refinement that can take the population into a world unaffected by environmental variation. Strategically, the population should not refine randomly, but concentrate on one or two behaviours and improve them as long as refinement pays off. Once the population has settled on a couple of trajectories of refinement in which it has invested many moves, the only rational strategy for an individual is to copy the refined behaviours and potentially refine further, rather than try to start over with a new behaviour that will never pay as much. Obviously, the individuals themselves are born naïve, not knowing how refined acts are in the population – nevertheless, attempting to copy the best refined acts is the optimal individual strategy. Thus, the cumulative setting creates an extra pressure for convergence, as copying is much more crucial for performance than in the other extensions if highly refined behaviours are available to copy.

This extreme convergence leads the population to use the same one or two behaviours at a time. This results in a pattern in the population that resembles conformity, even in the absence of an explicit conformist bias. This is not an isolated result (Franz and Matthews, 2010; L Rendell *et al.*, 2011). Using methods very similar to the ones used here, Rendell et al. (2011) showed that in the first Social Learning Strategies Tournament, the population converged on a smaller set of acts as a result of learning the beneficial behaviours. The authors found that this convergence becomes less strong when the environment changes faster, as the beneficial acts become obsolete faster, and updating and learning new information is necessary. Here we have shown that this convergence is even stronger in a cumulative culture setting – we confirm these results through empirical approaches in the next chapter.

Therefore, the evidence points towards the fact that in a well-defined problem space, strategic individuals can naturally come to acquire the same behaviours simply because they successfully learned what the best behaviours are. This learning is often mediated by copying, and a cumulative setting provides increased incentive to copy, because in a cumulative setting discovering or creating, through refinement, successful solutions alone is especially difficult, but copying is easy. As a result, the population converges on similar behaviour and, depending on the strength of copying, this similarity of behaviour can be so high that the pattern that emerges in the population can be easily confused with what we would expect conformist bias to lead to. This would therefore indicate a more complex interaction between cumulative culture and conformity (or at least population level patterns consistent with conformity) than currently suggested by the literature (Boyd and Richerson, 1985; Chudek and Henrich, 2011).

The pressure to copy created in the cumulative extension discussed here incentivises credulity. Copying is so much more beneficial for individuals that, in a refined world where everyone is using the refined behaviour, individuals should blindly copy rather than try to refine on their own. This situation relates to the trade-off between social learning and credulity that Boyd and Richerson (2009) discuss. According to these authors, social learning allows populations to accumulate adaptive knowledge through cumulative culture, and this requires them to often copy opaque technologies and norms without necessarily understanding how they work. This credulity, though, would also lead to the accumulation of maladaptive beliefs and practices. The trade-off is, then, between copying too little and potentially missing out on adaptive knowledge, and copying too much and potentially acquiring unsuitable behaviour. Boyd and Richerson claim that the optimum in the case of humans has led to substantial cultural transmission.

There is some evidence in humans that blind copying of social norms is indeed taking place (Henrich and Henrich, 2010), and Joe Henrich fully supports credulity as key to the evolution of human society and our success as a species (Henrich, 2016). According to him, our success in colonising virtually the entire planet is not due to individual human intelligence, but due to small incremental improvements in knowledge supported by cultural transmission and population dynamics. In this view, improvement over generations relies on blindly copying opaque technology and knowledge – if individuals did not show this level of credulity, faithful transmission would be impossible, which would hinder cumulative culture. However, it still debated whether humans are blind or selective copiers (Enquist and Eriksson, 2007; Enquist and Ghirlanda, 2007), or whether pure copying even is the main mode of learning (Morin, 2015, 2016). We expect that, depending on context, domain, and circumstances, humans would rely more or less selectively on replicative social learning.

Although much more realistic than most analytical models in the literature, the tournament still greatly simplifies real-world phenomena. For the cumulative extension, we focused on a type of refinement that, like human culture, would allow a population to overcome environmental variation. In this case, the rational response is for the whole population to converge on one or two behaviours. However, this drastic convergence is not entirely characteristic of human culture. Human populations show remarkable variation in their cultural repertoires, which are a great deal smaller than the whole of human cultural knowledge. This contrast forms something of a paradox in the tension between convergence in the tournament and diversity in the real world. We could, then, imagine a scenario in which extreme environmental change events, or mass migration, could render the current cultural repertoire useless. In this case, the population would need to maintain more cultural diversity in order to have useful behaviours to fall back on, like in the other two extensions.

We focused on refinement here, but clearly there are other processes involved in cumulative culture that display different dynamics. Recombination, for example, is one aspect that has been claimed to rest at the heart of cumulative cultural evolution (Boyd, Richerson and Henrich, 2011b), yet little effort has been spent exploring it. This is due mostly to the fact that recombination cannot be modelled as straightforwardly as refinement, and most experimental tasks used so far do not allow for recombination (though see Derex & Boyd, 2016 for a first attempt in this direction, and the following chapter). We can easily imagine that, were we to focus on recombination, we would find increased variation, as opposed to the strong convergence we found here. This interplay between different processes involved in cumulative culture could explain the fact that, despite the convergence we witness in the cumulative extension, real world human culture is actually characterised by an astonishing amount of diversity. Thus, a complete account would look beyond the approaches current literature has been focusing on, and endeavour to take into account the full range of processes that contribute to cumulative cultural evolution.

Chapter 3

Behavioural Homogeneity without Conformity in Cumulative Culture

Abstract

Cumulative culture, the ability to build progressively on the achievements of previous generations, is a central aspect of human uniqueness, but experimental investigations of this phenomenon do not currently extend beyond simple tasks and small populations. I studied the dynamics of cumulative culture in a realistic setting with a large-scale dataset of computer code obtained from a series of collaborative programming competitions involving hundreds of participants run over a 14-year period. Participants submitted solutions to a non-trivial computational problem, and the submitted solutions were then made available to all for use in subsequent submissions. I quantified the extent to which copying took place, and its consequences on the diversity of culture. As improvement in the complex tasks became progressively more difficult with the accumulation of more valuable information, populations largely focused on copying and improving the current best entry. As a result I observed patterns of convergence, punctuated by jumps from one idea to another. This convergence lead to a decrease in cultural diversity over time, as the population focused on solutions that have already benefitted from improvements made by many participants. We conclude that when complex solutions are built over time through cumulative culture, conformity as a population outcome need not depend on cognitive processes that drive individuals to copy the majority. Instead, it could simply be an emergent pattern in a population of individuals independently copying in a cumulative culture context. The question of whether this emergent conformity is in any sense an optimally adaptive approach to complex problems remains open.

3.1. Introduction

The cultural transmission of knowledge and skills, and concomitant advances in technology, have led to incredible demographic and ecological accomplishments in our species (Mathew and Perreault, 2015), but the key aspects that set human culture apart from anything seen in non-humans are still to be definitively identified. Proposed as a crucial element for this distinction, cumulative culture is the accumulation of knowledge over time, often associated with an increase in efficiency or complexity, and leads to a "ratchet" effect that allows populations to construct incrementally improved technologies that could not have been invented by a single individual, yet which are maintained over generations (Boyd and Richerson, 1985, 1996; Tomasello, Kruger and Ratner, 1993).

A set of cognitive processes that include teaching, language, imitation and prosociality seem to allow this uniquely human accumulation of knowledge (Boyd and Richerson, 1985; Galef, 1992; Tomasello, 1999; Laland, 2004; Tennie, Call and Tomasello, 2009). Notably, human reliance on imitation has received support as a key element of cumulative culture (Caldwell and Millen, 2009; Tennie, Call and Tomasello, 2009; Lewis and Laland, 2012; Derex, Godelle and Raymond, 2013); but see also (Marshall-Pescini and Whiten, 2008), yet a recent comparative study on cumulative improvement seems to indicate that this factor is not uniquely important. Rather, humans seem to rely on a package of social cognitive capabilities, encompassing teaching (largely through verbal instruction) as well as imitation and altruism (Dean *et al.*, 2012).

Additionally, spurred by the observation that bigger populations sustain larger and more complex sets of cultural adaptations (Shennan, 2001; Powell, Shennan and Thomas, 2009; Kline and Boyd, 2010), a large amount of research effort has gone into investigating the relationship between population size and cultural complexity. As discussed in the introduction, population size, sociality, and demography have all been proven to be a facilitators of cumulative culture through theoretical modelling (Henrich, 2004; Enquist and Ghirlanda, 2007; Enquist *et al.*, 2010; Lehmann, Aoki and Feldman, 2011; Kobayashi and Aoki, 2012; Pradhan, Tennie and van Schaik, 2012; Vaesen, 2012), experimental approaches (Caldwell and Millen, 2010; Derex *et al.*, 2013; Muthukrishna *et al.*, 2013; Kempe and Mesoudi, 2014), as well as field studies with real populations (Kline and Boyd, 2010; Collard, Ruttle, *et al.*, 2013) .

Despite these insights, methodological limitations still restrict our knowledge of the drivers and dynamics of cumulative cultural evolution in contexts that approach modern complexity levels. On the one hand, the modelling work in this field typically operationalizes cumulative culture as either an increase in the number of cultural traits in the population (Enquist and Ghirlanda, 2007; Strimling *et al.*, 2009), or an increase in skill level in a single trait (Henrich, 2004), but struggles to capture the complexity of interaction between traits that characterize cumulative culture (although see (Enquist, Ghirlanda and Eriksson, 2011) for a first suggestion in this direction). On the other hand, experimental approaches have been forced to focus on highly simple cases.

For instance, Caldwell and Millen (Caldwell and Millen, 2008) adapted a long-standing micro-society paradigm to simulate inter-generational transmission in the study of cumulative culture (Mesoudi and Whiten, 2008; Hoppitt and Laland, 2013). Groups of participants tried to solve simple tasks such as building paper airplanes or spaghetti towers – some building, some observing. After a fixed period of time the observers became builders, and the builders were replaced by naïve observers. The experiments showed that, even in such simple conditions, chains improve over generations, and even show descent with modification, as designs became more similar within chains than across them. These studies have been criticized however as using too simple a task, which might affect the results and the conclusions that can be drawn regarding cumulative cultural evolution (Derex *et al.*, 2013; Muthukrishna *et al.*, 2013).

Subsequent studies have adapted this microsociety design to more complex tasks like building an intricate fishing net or arrowhead, or reproducing a complicated graphical symbol or knot (Derex, Godelle and Raymond, 2013;

Muthukrishna *et al.*, 2013; Derex *et al.*, 2015; Derex and Boyd, 2016). These results are in line with theoretical predictions, suggesting that cumulative cultural evolution relies crucially on larger population sizes and process information, yet there is still a large gap between these experimental settings and real-world cumulative culture, especially with regards to exploring the interactions between a large number of participants in a complex task that allows for open-ended improvement.

The challenge in finding an appropriate task is that one of the defining characteristics of cumulative culture is its overwhelming complexity – it typically involves material artefacts that are constructed using opaque techniques and processes, which consist of a complex interaction of traits that cannot be easily reproduced (Oswalt, 1976). These artefacts are typically used to find the best solution in multimodal adaptive landscapes (Mesoudi, 2008), where the best solution is unclear and very difficult to find, such that the relationship between traits and payoffs is obscured. It is difficult to anticipate how well the results of laboratory experiments to date hold when complexity scales up to levels comparable to human culture today. As population size increases, for example, so does the cost of filtering information and discriminating between payoffs. In this context, the deployment of social learning strategies which dictate how individuals learn from each other could critically affect the distribution of traits in the population and the rate of change of these traits (Laland, 2004; Rendell *et al.*, 2010).

The recombination of already established cultural traits is also thought to play a central role in cumulative cultural evolution (Basalla, 1988), along with other innovative mechanisms such as modification and invention, as key processes contributing to improving culturally transmitted information and leading to cultural ratcheting (Tomasello, 1999). While the fidelity of transmission has been studied extensively in the cultural evolution literature, as discussed in Chapter 1, very little is understood about how creativity shapes cumulative culture. Lewis and Laland (2012) introduce one of the few theoretical studies investigating the role of cultural recombination in cumulative culture. They used a model to show that invention, combination, and modification rates are much less important to cultural accumulation than the fidelity of transmission. Enquist et al. (2011) used a more complex theoretical paradigm to investigate how different models of interaction between cultural traits lead to different population-level dynamics of cultural evolution in terms of the increase in cultural complexity and cultural diversity between populations. The authors showed that recombination leads to a much faster increase in cultural traits than successive modification or differentiation. Combining already existing cultural traits decreases similarity between different populations, and largely increases cultural complexity through an increased rate of innovation that can mitigate cultural loss.

An empirical study by Derex & Boyd (2016) incorporated recombination as the key process involved in cumulative culture. The authors designed a task that relied on pre-determined triadic combinations starting from a set of six ingredients in order to invent increasingly more rewarding 'remedies', which could in turn be used in recombination. The number of possible combinations increased quickly, and early innovations directed participants on divergent trajectories, such that partially connected groups were more successful at discovering all innovations than fully connected groups. However, this result relied on pre-defined cultural trajectories. Similarly, the types of micro-society experiments reported above used tasks that are generally not suited to allow for recombination to take place freely, although one study found evidence that when presented with five model artefacts, participants tend to copy the best performing one, while also including elements from the less effective ones, suggesting recombination (Muthukrishna *et al.*, 2013). Recombination becomes a real possibility in a larger population when devising novel solutions to problems – and indeed is something that people readily seem to do – but current experimental approaches restrict its investigation.

Separately, the role of conformity in cultural evolution is currently subject to considerable debate regarding the degree to which it is adaptive, and the extent to which humans and non-human animals actually do conform (see Morgan & Laland, 2012; van Leeuwen & Haun, 2014 for reviews). Conformity has been approached by both the psychology and the cultural evolution literature with slightly different focus – while psychology is mostly interested in the conditions under which humans change their behaviour in order to match the majority, cultural evolution is concerned with naïve individuals and the circumstances under which they come to acquire the majority behaviour (van Leeuwen and Haun, 2014).

The literature makes a distinction, in terms of the cognitive mechanisms underlying conformity, between normative conformity (i.e. individuals acquire the majority behaviour in order to affiliate with a group) and informational conformity (i.e. individuals acquire the majority behaviour as a shortcut to acquiring useful information; van Leeuwen & Haun, 2014). The cultural evolution literature is mostly interested in the latter - conformist traditions can have substantial fitness benefits to the extent that they facilitate the spread of locally adaptive behaviour (Boyd and Richerson, 1985; Henrich and Boyd, 1998). Conformity provides a possible explanation for cultural diversity, as it both increases homogeneity within groups and heterogeneity between groups, and it could thereby promote cultural group selection (Richerson and Boyd, 2005). What has been much less considered is how conformity interacts with cumulative culture, and whether there are situations in which the dynamics of cultural evolution can lead to behavioural homogeneity at the population level (i.e. low diversity in behaviour) without actually requiring an explicit conformist learning bias. Here I show how a history of investment in complex solutions in a cumulative cultural evolution context can lead to such outcomes. This distinction is relevant in relation to the cultural group hypothesis theory, which suggests that large-scale co-operation can evolve as a result of inter-group competition (Boyd and Richerson, 1985).

In this chapter I introduce a new tractable method of observing cumulative cultural evolution on a fine scale in a real-world context that reflects the complexity of human behaviour. I analysed cumulative cultural evolution in a large-scale dataset of computer code originating from collaborative programming competitions organized over the course of 14 years. The dataset reaches a level of complexity that has not been achieved by previous experimental investigations of cumulative culture. I was particularly interested in the dynamics of cumulative cultural evolution, how copying biases and behavioural variation interact in a cumulative setting, and how these factors impact population outcomes such as the diversity of culture.

3.2. Methods

3.2.1. Dataset

The dataset resulted from a series of 19 online competitions, organized by MathWorks, the software company that produces the MATLAB technical computing package. In every contest the organisers set a computational challenge and, over the course of one week, participants developed and provided solutions in the form of MATLAB code (see Appendix for a full list of the contests and additional information on the challenges). Upon submission, entries were evaluated and, if they ran successfully, assigned a score that was a composite of the effectiveness of the solution, the complexity of its code, and its computation time. Once an entry had been evaluated, its score, code and the username of the participant who submitted it became public and available to all the other participants. Participants could submit as many solutions as they wanted though an online interface, within which they were identified by a self-chosen nickname. Although submission was completely anonymised, participants generally submitted solutions from a single ID, because the main motivation to win the contest was reputational – actual prizes were nominal, for example a branded T-shirt. We did not directly collect demographic data on the participants, but they were generally Western males who use MATLAB professionally either in academia or in the industry. There was however scope for a wide range of experience levels and not all participants were MATLAB experts.

The challenges were all NP-complete computer science problems (Karp, 2010), meaning an algorithm cannot find exact solutions on feasible timescales for problems of decent size. For example, one contest was based around a 'Crossword' problem where participants were given a list of acceptable words, each associated with a score and a grid size, and were asked to provide a grid that maximises the number of high value words. Another contest proposed a generalised Sudoku problem, in which participants were provided with a partially filled grid and a list of numbers, and had to fill in the grid so that each row, column, and region add up as close as possible to the same target sum. Using this type of optimisation problems results in reliance on heuristic and approximate solutions, thus allowing for open-ended improvement in the task. Our sample included 19 contests, with an average of 2396 entries per contest (ranging from 1138 to 6367 entries) and an average 120 participants per contest (between 63 and 202). This amounted to a total of 47,967 entries containing a total of 483,173 lines of code (between 1 and 2757 lines per entry). Each contest resulted in a database containing every line of every code entry submitted, along with the entry's author, time of submission, and score on the particular problem set in that contest (see Appendix for an example).

There were a number of variations on this basic model. In 2004, the organisers introduced two more stages to the competition. While the first 6 contests allowed participants to view other entries from the beginning, the subsequent 13 contests used a framework consisting of three stages. On the first day, 'darkness', participants did not have any information on the scores of their own entries or other players'. During the second day, labelled 'twilight', participants only had information on the rank of their own entries compared to everyone else's. From the third day onwards, in 'daylight', they had full access to information concerning their own entries and the entries of other players, including their score, rank, and computer code. When analysing the data from these later contests, I only included data from the daylight condition – the only condition directly comparable with earlier contests – while statistically controlling for this difference using mixed effects models.

Entries in the contests were scored as a function of their result on the task, the speed of execution, and code complexity, measured using McCabe's cyclomatic complexity (McCabe, 1976) which takes into account the code structure by measuring the number of independent paths through a program's source code. The score was given by

$$score = k_1 * result + k_2 * e^{k_3 * runtime} + k_4 * max(complexity - 10, 0)$$

(Equation 3.1)

The values used for the *k* variables were $k_1 = 1$; k_2 in the range 0.1 – 0.2, $k_3 = 0.05$, and k_4 several orders of magnitude smaller. The first two factors weighed more heavily towards the final score, while limiting complexity ensured that entries remain concise so as not to lock up the computer evaluating the entries. Thus, improving task result score, or the speed of execution, or both, could all result in better contest scores. Entries were disqualified if they exceeded execution time or length limits.

3.2.2. Measuring similarity between entries

In the contest microcosms, the use of code from previous entries represents cultural transmission. As part of the submission procedure, participants had the option to declare a "parent" entry, i.e. entry they were inspired by or they decided to copy. This is a self-declared measure of copying, and so vulnerable to innacurate reporting, but here I also tracked transmission directly by tracking lines of code across entries.

The code similarity between two entries was used as an index of copying – the higher the similarity between two entries, the higher the chance the later submitted entry copied the earlier one. The similarity between entries over time was measured in terms of lines of shared code. In computer code, some structural keywords (such as 'for' and 'end' in MATLAB code) are identical, and when lines contain only such keywords, then similarity between those individual lines can have little to do with copying. In our dataset such single-keyword lines comprised 13% of the total number of lines submitted. However, most lines of code also refer to variables – arbitrary symbolic names chosen by the coder and linked to values that can change – and the probability of using identical variable names by chance is extremely low. For this reason, most lines of code that are identical are very likely to have been copied. Of course, while copying implies similarity, the inverse is not necessarily true. While two participants are unlikely have developed very similar solutions by chance, more plausibly it could be the case that two entries share a high similarity because both have copied an unrelated third entry. This similarity would however still be relevant for this work, as the interest is not in the specific copier and model, but rather in the relative probabilities of an entry introducing predominantly novel information or reusing code already existing in the population.

I used a variation of the Sørensen–Dice coefficient in order to measure the similarity between two entries (Dice, 1945; Sørensen, 1948). Originally a statistic designed for comparing two ecological samples in terms of presence/absence of species, it has an extension, the Czekanowski similarity (Bray and Curtis, 1957), which does not take into account merely presence/absence, but incorporates the actual frequency of each sample, thus including more information about the overlap in samples between species. The similarity, which we use here, is given by:

$$CZ_{ik} = 2\,\frac{\sum_{j=1}^{S}\min\,(x_{ij},x_{kj})}{\sum_{j=1}^{S}(x_{ij}+x_{kj})} \quad \text{(Equation 3.2)}$$

where CZ_{ik} is the similarity between samples i and k, x_{ij} is the number of instances of species j in sample i, and x_{kj} is the number of instances of species j in sample k. For our analysis, each sample corresponded to an entry, and each species is a line of code. Every entry is a set of lines of code, so the similarity between two entries was a function of the total number of lines they had in common, including reoccurring lines, relative to the sum of their lengths.

The Czekanowski similarity does not take context into account – it relies on the number of lines, disregarding order and potential sequences of lines that might reappear together – yet it performs very well for our purposes (during exploratory analysis I tested several similarity measures, including more comprehensive character-based measures like Levenshtein distance, and found very comparable results). If two entries have a high Czekanowski similarity, they are almost certainly similar in terms of the order of lines of code, as it is extremely unlikely that the same lines could be combined differently in a piece of code that remains functional. Moreover, the nature of computer code ensures that the lines in an entry will be highly idiosyncratic because variable names are arbitrarily selected from a vast sample space (MATLAB variable names can be up to 63 characters long, and can contain letters, digits, and underscores, resulting in 10^{97} possible variable names, approximately), so the chance of finding the same lines in two entries that are not actually functionally identical is very low. Thus the Czekanowski similarity between two unrelated entries will be low, while two functionally related entries would exhibit high Czekanowski similarity.

3.2.3. Assessing the relationship between similarity and performance

I expect that copying will be associated with better performance, so in order to investigate whether code similarity is indeed linked to improvement in score, I used code similarity to the current leader as a relative measure of copying, and the difference in score between each target entry and the current leader as a relative measure of improvement in task. I split entries in leaders, i.e. entries that manage to achieve the best score at the time of their submission and therefore improve the overall score, and the rest, in order to establish whether successful entries use novelty differently. Because the data was highly skewed and non-normally distributed, I tested the relationship between improvement and similarity in both leaders and the rest using non-parametric Spearman correlations between the two variables of interest, rescaled as values between 0 and 1 in order to enable cross-contest comparison.

Additionally, I fit a quadratic linear model with score difference as the dependent variable (this was rescaled a value in the range of [-1,1], such that leaders were associated with positive score increments, and the rest of the entries were associated with negative score differences), and the similarity to the current leader as a main and quadratic effect, both including an interaction with a factor indicating whether the entry was a leader. In order to control for the non-independence of entries submitted in the same contests, or by the same participants, I included contest as a random effect, and author as a random effect nested within contest. The expected value of the increment for entry k submitted by author j in contest i is specified in the model definition is given by:

$$E(Increment_{ijk}) = \alpha + \beta_i + \gamma_{ij} + \beta_1 Similarity_k Leader_k + \beta_2\ Similarity_k^2\ Leader_k$$

$$\beta_i \sim N(0, \sigma_1^2);\ \gamma_{ij} \sim N(0, \sigma_2^2)$$

3.2.3. Analysing cultural diversity

I expect that similarity will increase over time as a result of copying, which will lead to a decrease of cultural diversity over time. To measure diversity I grouped entries to create snapshots of the ‘culture’ (the collection of solutions submitted) of the population at given points in the contest. I sorted entries by order of submission and grouped them in bins each containing 1% of the entries in the contest, then computed a diversity measure for each bin. This measure over the contest reflects the diversity of the first 1% of the entries, the following 1%, and so on. Within each bin, diversity was measured as the number of unique lines of code entered divided by the total number of lines submitted in the contest, thus resulting in values ranging from 0 to 0.046, with a mean of 0.004258 and median of 0.00755.

The bins were numbered from 1 to 100. Since the entries were ordered chronologically, and since the analysis was not concerned with the exact time of submission, but with how diversity changes during the contests, I used bin number as our time measurement. I also performed a separate analysis with time of submission as the explanatory variable, not presented here. This analysis suggested that there was less activity at the beginning of each contest and considerably more submissions towards the end. Therefore the time measure using bin number is conservative, as it compresses the initial time period of high diversity, and expands the final lower diversity (and potential noise), thus potentially reducing the effect of time on diversity.

I fitted a Bayesian mixed-effect regression model using Monte Carlo Markov Chain (MCMC) methods to estimate the parameters with JAGS (Plummer, 2003) in R (Team, 2016). As diversity is measured as a proportion between 0 and 1, I used beta distributed errors, with a logit link. I used diversity as the dependent variable, and chronological bin number as a fixed effect. Each contest proposed a different problem and had a different set of participants, which meant that entries from within the same contest could not be considered independent. To account for this I included normally-distributed random effects, allowing both the intercept and the slopes in the diversity-time relationship to vary with contest. The model definition, parameterised as per Ferrari & Cribari-Neto (Ferrari and Cribari-Neto, 2004) is given below:

$$Y_{ij} \sim beta(\mu_{ij}, \phi);\ E(Y_{ij}) = \mu_{ij};\ var(Y_{ij}) = \frac{\mu_{ij} \times (1-\mu_{ij})}{(\phi+1)}$$

$$\text{logit}(\mu_{ij}) = \alpha_j + \beta_j \text{Bin}_{\text{ij}};\ \alpha_j \sim N(\mu_{int}, \sigma^2_{int});\ \beta_j \sim N(\mu_{slope}, \sigma^2_{slope})$$

I present results from an MCMC run of 50,000 iterations after burn-in, with 3 chains, and a thinning value of 10, resulting in 5000 posterior samples, with adequate mixing. I used uninformative Gaussian priors for the μ estimates, and flat uniform priors for ϕ and σ: μ ~ N(0, 0.001), ϕ ~ U(0,1000), σ ~U(0,1000).

3.3. Results

3.3.1. Copying and scores

Participants copied each other considerably: all entries contained at least one line of code from a previous submission, and on average only 3.8% of the entries consisted of at least 50% novel lines (Fig.1). Each contest produced a collection of code artefacts that evolved over time through gradual modifications by multiple individuals – each contest was therefore a microcosm of cumulative culture, in which progressive improvements by many individuals result in a cultural product – a computer code function – that improves over time in a quantifiable way.

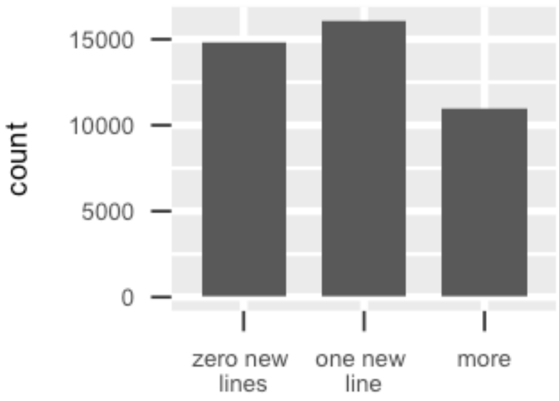


Figure 3.1 – total number of entries introducing none, one, or more new lines of code into the contest. Most entries clearly introduce new information

As expected under a cumulative cultural setting, the scores did in fact consistently improve throughout all contests (on average the best solution scored 40 times better than the first), thus the population as a whole became more effective at solving the task (Fig. 3.2). Improvement alone is not surprising, but along with the large amount of copying taking place it provides compelling evidence that these contests indeed simulate cumulative cultural evolution.

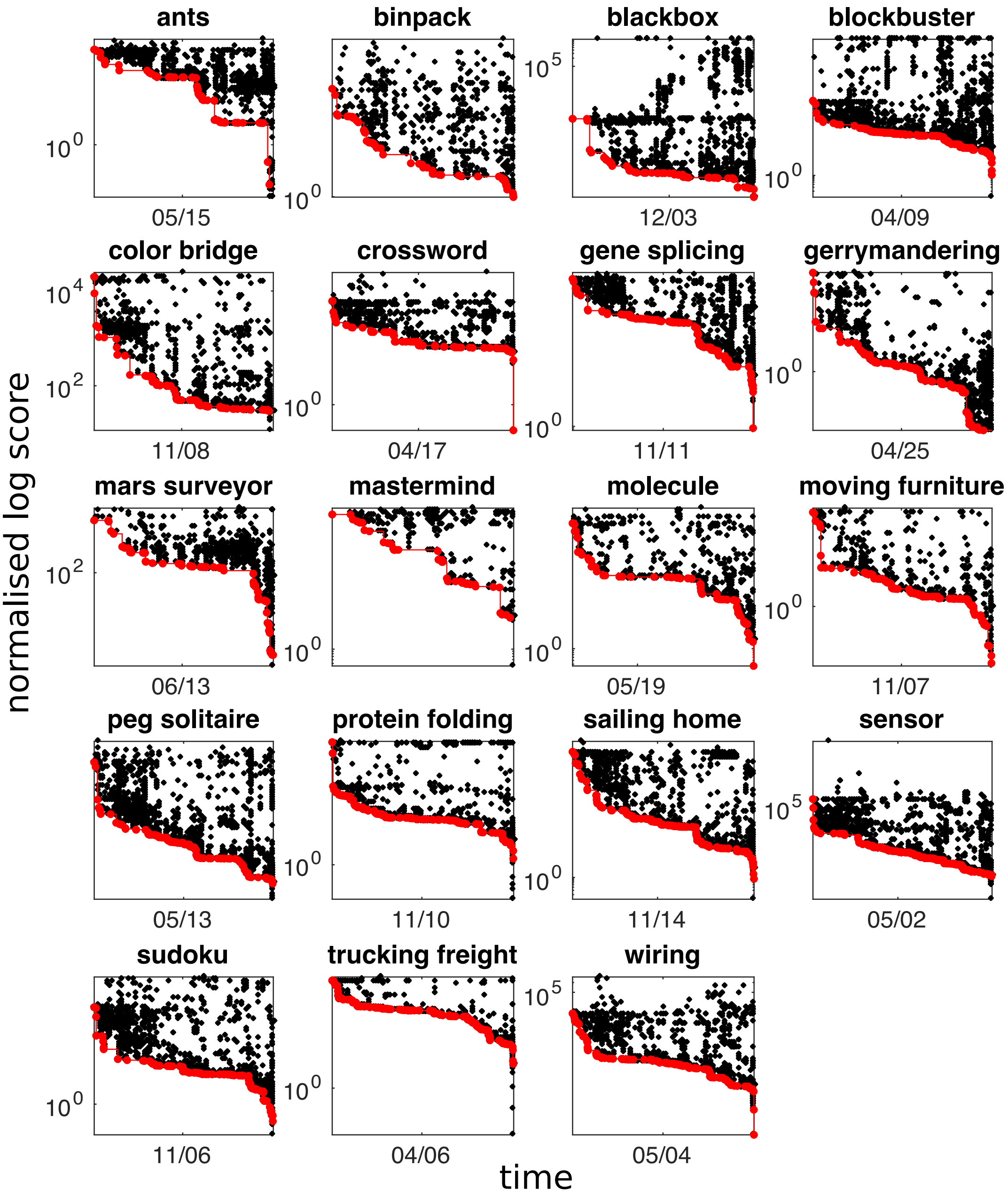


Figure 3.2 – Normalized log-transformed scores over time in all contests. Note that in all contests low score values are better. Each point on the graph is an entry. The red line follows the progress of the leading entries in the contest, i.e. the entries that achieved the best score at the time of their submission

Although the contest setup produced improvements that seem externally collaborative, it was still a competitive process. This is illustrated by the fact that some participants strategically held back their most promising solutions until the very end of the contest in order to avoid being copied and losing the potential best score. This artefact does not affect our conclusions – in fact, they still held even if I incorporated this final artificial spike in activity and diversity as noise in the analysis.

Crucially, only a very small proportion of entries improved upon the current leading score when they were entered (overall just 6%, Fig. 3.3). Thus each contest posed a genuinely challenging task. Some contests showed rapid score improvements in the initial stages, but not all did, and nearly all continued to show score improvements over the whole duration of the contest. Interestingly, there was large variation in the rate of improvement over time, with distinct periods of stasis characterised by minimal improvement in score, separated by large jumps in score associated with key innovations. Each contest had a unique history of improvement, which is precisely what we would expect under cumulative cultural evolution.

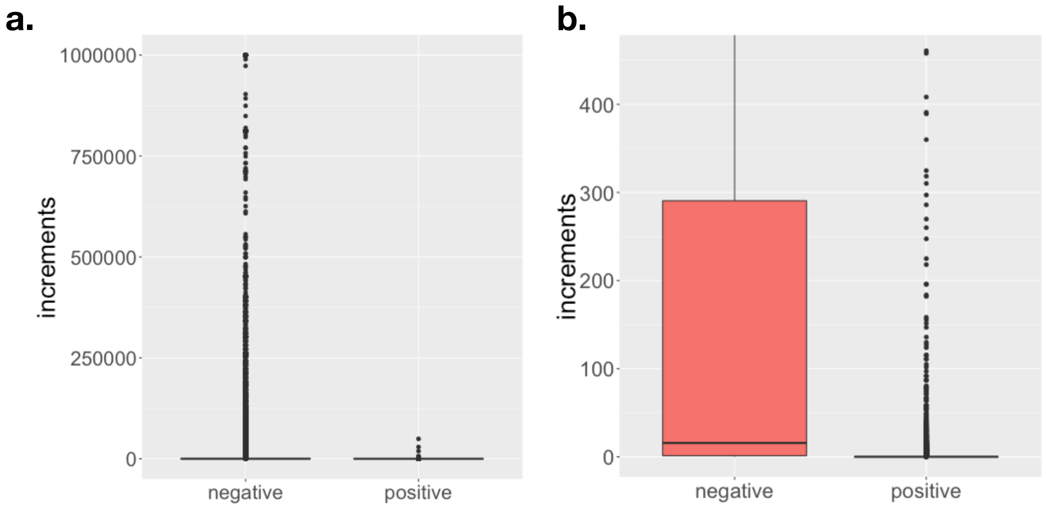


Figure 3.3 – distribution of negative/positive incremental change in score relative to the current leader in all the contests (a), and adjusted on data below the third quantile (b). Increments were calculated as the difference in score between the current best entry so far (i.e. the current leader) and each entry – as a lower score is better, positive increments represent entries that improve the overall score

3.3.2. Code similarity

I used a matrix of Czekanowski similarities between entries (Fig. 3.4-3.5, see Figure A1 for all contests) to illustrate the patterns of copying occurring throughout the contests. Copying grouped the submitted entries into clusters of highly similar solutions, illustrated by blocks of lighter colour in the plotted matrices. These matrices show how populations converge on particular forms of solution for periods of time, and occasionally switch to new ones. We can describe this dynamic in terms of tweaks and leaps: the population adopts a solution for a while, modifying and tweaking it, and at times leaps to a new solution that has low similarity to those preceding it. These patterns of tweaks and leaps vary between contests, yet all contests exhibit consistent periods of tweaking, where multiple players enter very similar solutions modified only in small ways, punctuated by leaps in ideas, when a new form of solution is introduced that takes the lead and captures the attention of other players.

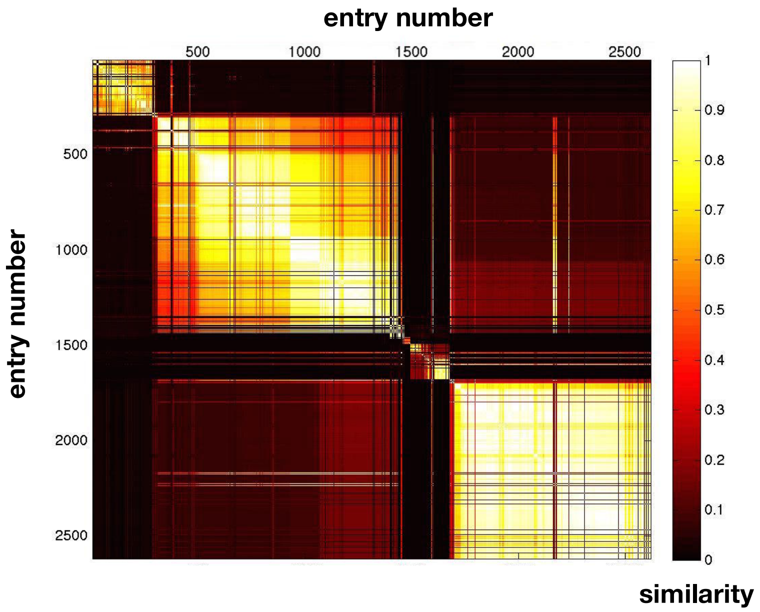


Figure 3.4 – Similarity matrix between all pairs of entries in one contest (for ease of interpretation this example includes only passed entries that declared a parent, but the trend is identical in the entire collection of entries). Entries are ordered chronologically from top to bottom and left to right. Each point represents the similarity between two entries, and each line the similarity between an entry and every other entry. Lighter colours indicate higher similarity (data from the contest 'Peg Solitaire', May 2007).

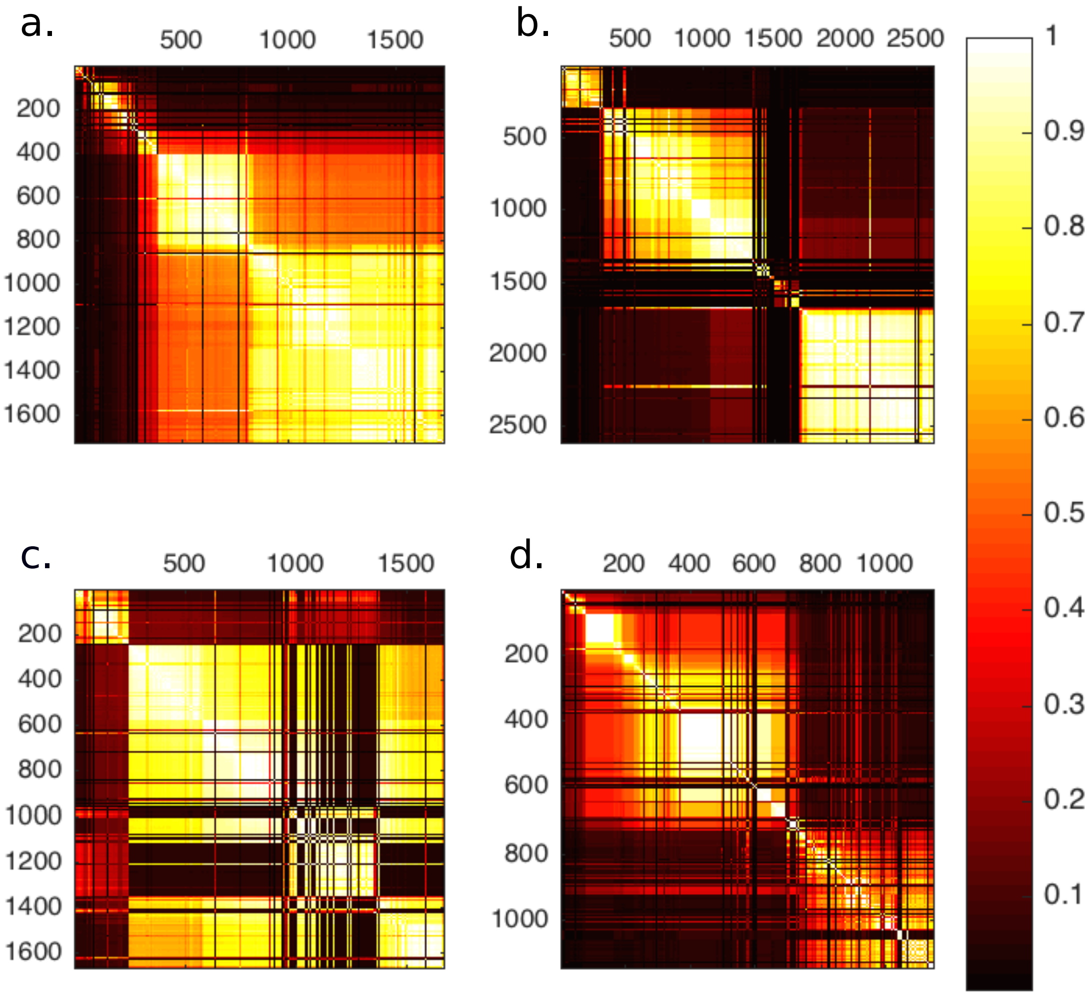


Figure 3.5 – Code similarity matrices between all pairs of entries in four contests. Entries are ordered chronologically from top to bottom and left to right. Each point represents the similarity between two entries, and each line the similarity between an entry and every other entry. The bright squares show series of entries that are relatively similar to each other compared to previous and subsequent periods, representing minor variations on a solution 'theme', while the bottom-right corners of the bright squares show where the population switched to a new form of solution that was relatively dissimilar to those that came before, and the top-left corners show where a new solution 'theme' began. Data for four contests: (a) 'Gerrymandering' – April 2004, (b) 'Peg Solitaire' – May 2007, (c) 'Color Bridge' – November 2009 and (d) 'Mars Surveyor' – June 1999. The variation in patterns of tweaks and leaps illustrates how sometimes ideas are based on older ones – the final large group of similar solutions shows intermediate similarity to the previous smaller group (a), while other times the population switches to a completely new idea – the three main groups of similar solutions are clearly distinct (b). In some cases the population reverts to a previous idea – illustrated by very high similarity between the final group and a previous one (c). Some ideas last in the population for a long time as characterised by large succeeding groups of similar ideas (a), yet sometimes contests are characterised by rapid shifts in ideas (d).

Copying was not indiscriminate. Participants preferentially copied the current leader compared to random copying: the baseline distribution of similarities between all entries shows a clear skew towards zero (Fig. 3.6a), but the similarities to the current leader peaked around the maximum value (Fig. 3.6b), indicating that most entries copied the current leader. While 50% of the entries had a similarity > 0.9 to the current leader, only 26% had a similarity of this level to more recent entries submitted since the current leader. Therefore entries were much more likely to be similar to the current leader than any other entry. This pattern becomes even stronger in entries that took the lead when they were submitted (Fig. 3.6c): 91% of these leading entries had a similarity of at least 50% to the previous leader, suggesting that remarkably few new leaders introduced substantial amounts of novel code. Copying the leader was then a recipe for success. The distribution of similarities to the current leader (Fig. 3.6b) was not only dominated by high similarities, but clearly skewed toward extremes – most similarities were either very high or very low with very few intermediate similarity entries.

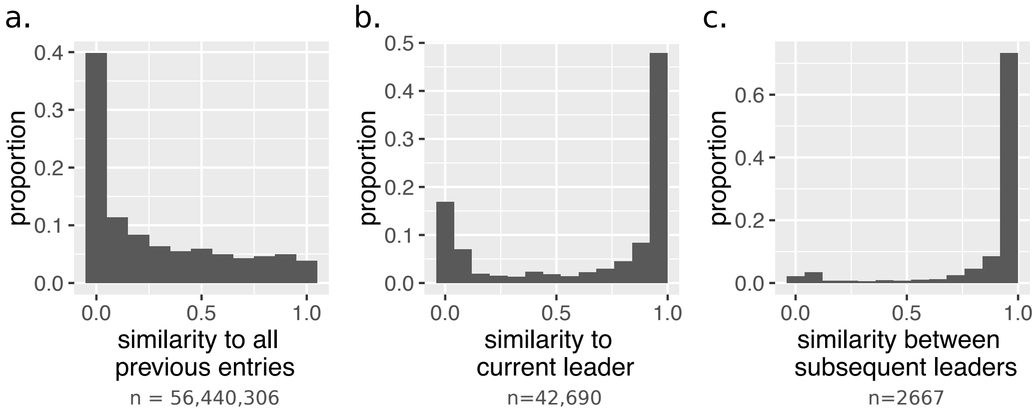


Figure 3.6 – (a) proportion of similarities between all entries; (b) to the current leader when the entry was submitted; and (c) of those entries that took the lead when entered compared to the previous leader, across all contests

The success of an entry – whether it took the lead (i.e. scored better than anything previously submitted to the contest), and if so by how much – had a complex relationship with the extent to which it was based on copying or innovation. Overall and fairly unsurprisingly, the more similar an entry was to the current leader, the more similar the scores (Fig. 3.7). Entries that took the lead (i.e. the entries that beat the current best when submitted) show a significant negative correlation between similarity to the previous leader and their associated improvement in score (Spearman ρ = - 0.15, $p < 0.001$). In other words, in the context of these successful entries, a high similarity to the current best entry was associated with a small improvement, while leaps in ideas, indicated by low similarity to the current leader, were associated with large improvements.

While this was true for entries that took the lead the picture changes drastically when considering just the entries that did not take the lead. In this context, the correlation between the similarity to the current leader and the difference in score between the current entry and the current leader was even stronger (Spearman ρ = -0.53, $p < 0.001$). As this refers to entries that did not manage to improve on the overall score, large score differences represent particularly unsuccessful entries that scored considerably lower than the current leader, and are associated with more innovative entries. Thus, the more similar an entry was to the current leader, the more likely it was to be associated with a smaller change in score, whether negative or positive, while more innovative entries were associated with both large improvements in score, but also the most spectacular failures.

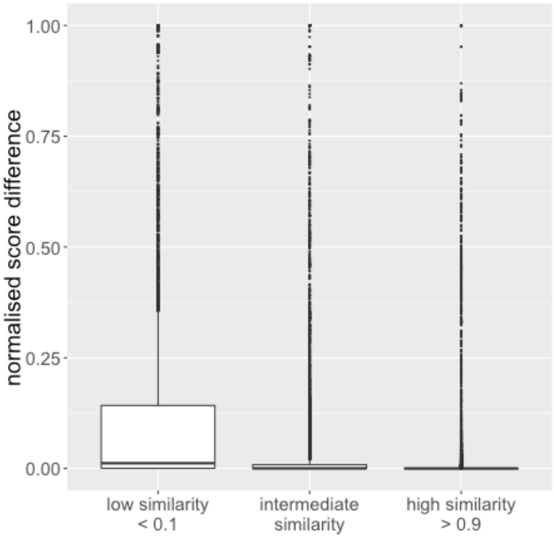


Figure 3.7 – normalised score difference between each entry and their current leader, as a function of code similarity to the current leader. The more similar an entry in terms of code, the smaller the difference in score.

This result was confirmed by the mixed linear model. Although the interaction between leader similarity and whether the entry was a leader or not was not significant, it seems that in the case of leaders, there is a trade-off in terms of how similarity to the leader relates to the score improvement. A solution needs to be similar enough to the previous leader, but not too similar, in order to achieve a high improvement. For non-leading entries, though, the highest increment (i.e. lowest score difference relative to the leader) is achieved with the highest code similarity, while low similarity is associated with drastic reduction in score. However, the data used for this model was bounded and heavily skewed, which means the model fit was modest and results from the model should be cautiously treated. Nonetheless, both methodological approaches point to the same results.

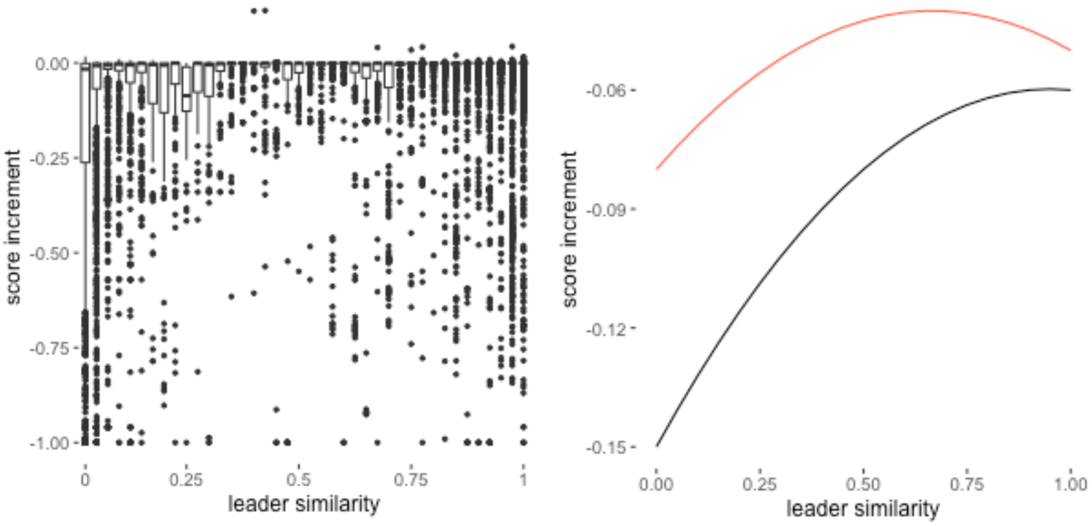


Figure 3.8 – (a) score increment (i.e. signed normalized score difference between each entry and the current leader) as a function of leader similarity in all daylight entries in all contests; (b) results from the quadratic linear mixed model for leaders (in red) and the rest of the entries (in black)

In the context of these programming challenges, then, copying is a ‘safe’ strategy, associated with relatively small improvements or decreases in score. On the other hand, innovation is risky – more often than not it leads to much worse scores than copiers are achieving – but when it is beneficial it is associated with larger improvements in performance. The ‘risk’ to innovators here is in terms of time wasted developing a new solution in contests that were heavily time constrained that proves worse than the current leaders, but is easily equated to real-world risks in real-world cumulative cultural evolution in competitive contexts. So, if we consider the current best entry to be the optimal choice at any given point in time, the safe choice in the contests is to copy the current leader – and it is clear that this is what most participants do. There are consistently large numbers of tweaks and relatively few leaps (Fig 3.4-3.5), and most entries exhibit high similarity to the current leader (Fig. 3.6).

3.3.3. Cultural diversity

I also investigated how cultural diversity changed over time. The results above show that many entries copied the current leader. As a result, the population converged on similar solutions for periods of time, causing a decrease in the diversity of culture, as measured by the normalised number of distinct lines of code present in the population during any given time interval (Fig. 3.9, 3.10; Bayesian mixed models with beta distributed errors indicated an average decline of 0.15; 95% credible interval [-0.19 to -0.12] in the logit of diversity for every additional 10% of contest entries, equivalent to a drop in diversity from 0.01 to 0.086. This is a drastic change considering the average normalised diversity value is 0.0042). While individual exploration is expected to be associated with a large variety of solutions, over time copying reduces the number of solutions the population as a whole is entertaining at a given time. Indeed, the distribution of all entry similarities to the current leader indicates that the majority of the population seems to be performing very similar behaviours (Fig. 3.6b).

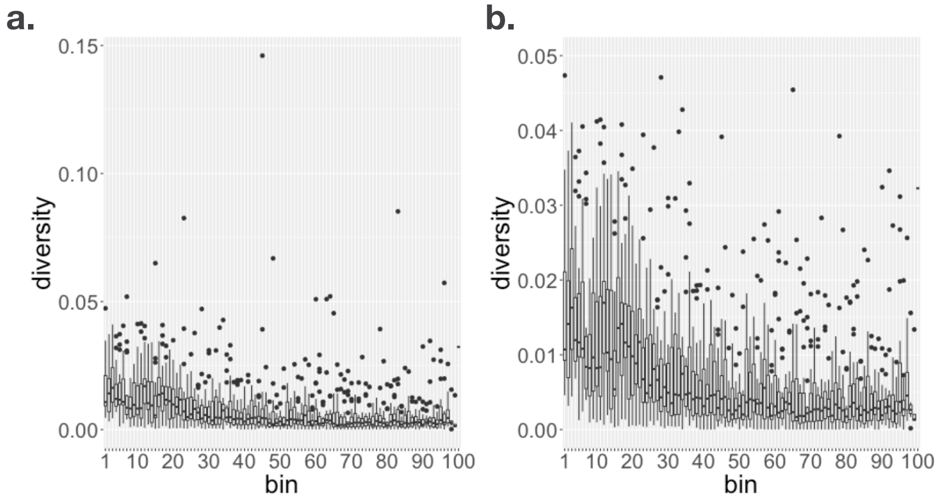


Figure 3.9 – (a) distribution of cultural diversity values across all contests for each 1% contest progress bin, and (b) adjusted to exclude outliers in

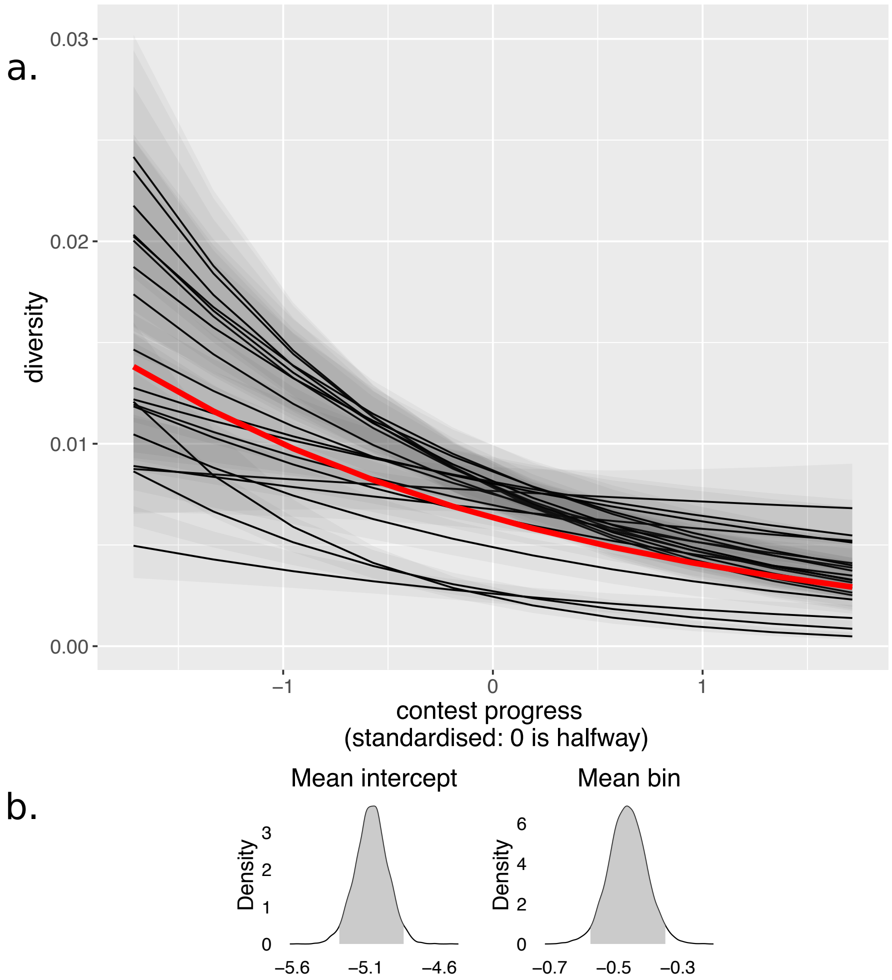


Figure 3.10 – (a) generalised linear mixed-model predictions of cultural diversity over time. Each black line plots the predictions for each contest, and the red line plots the overall estimate. The shaded area indicates the 95% credible interval of the posterior estimates per contest. (b) posterior distributions of parameter estimates for intercept and standardised bin

3.3.4. Recombination

Copying also affects how individuals combine ideas from previous entries. Because copying took place on such a large scale that no entry is practically entirely new, I have chosen to regard the introduction of all new code as innovation, and I define recombination strictly as an association of cultural traits that have already been present in the population. These results thus assume combination of new and old ideas as a distinct process from recombination. This dataset does not allow to distinguish between genuine and copied recombination, so instead I chose to focus purely on how old ideas are aggregated in new entries and how they persist in the population. This analysis used a line-based approach – for each entry, I tracked each line back to the first 'parent' entry that introduced it into the contest. Thus each entry could be characterised in terms of its number of such parents. This essentially allows us to quantify how many original sources each entry draws inspiration from, and how long these persist over time.

Using this approach, entries drew on a large number of sources overall (Fig. 3.11a). The amount of recombination increased with time (Spearman ρ = 0.53, $p < 0.001$) and the length of the entry (Spearman ρ = 0.64, $p < 0.001$), but it was also positively correlated with the similarity to the current leader (Spearman ρ = 0.44, $p < 0.001$) and negatively correlated with the difference in score to the current leader (Spearman ρ = -0.25, $p < 0.001$). In order to test these relationships, because the absolute values for all measures (time, length of entry, similarity to current leader, and difference in score relative to current leader) depend on the contest, they were normalised within contest and rescaled to the interval [0,1] according to Equation 3.3 to allow for comparison between contests.

$$X' = \frac{X - X_{min}}{X_{max} - X_{min}} \quad \text{(Equation 3.3)}$$

The number of original sources was similarly rescaled within contest. As before, I did not use absolute time measurements, but instead I used the chronological order of the entries in the contest as a measure of time (such that time is an integer between 1 and the total number of entries submitted in each contest). Therefore, copying notably leads to an accumulation of recombination in the population – with time, entries borrow from more sources, and the use of more ultimate sources was correlated with better performance (Fig. 3.12).

Alternatively, individual recombination can be measured at the line level by tracking each line to the most recent previous entry that used it. It could be the case that an individual did not copy the last instance of a line being used in the contest, but they copied a previous entry. Therefore this is a conservative measure that assumes copying is the dominant strategy, and that entries tend to copy the latest entries. 90% of all entries drew on 5 sources or fewer, while 25% modified only one previous entry, so did not actually use recombination by the definition used here. For comparison, only 5% of all entries drew on 5 original sources or less, indicating recombination involved a much larger number of sources at the population level. So although the population accumulated recombinations over time, individual solutions were based on a small number of proximate sources.

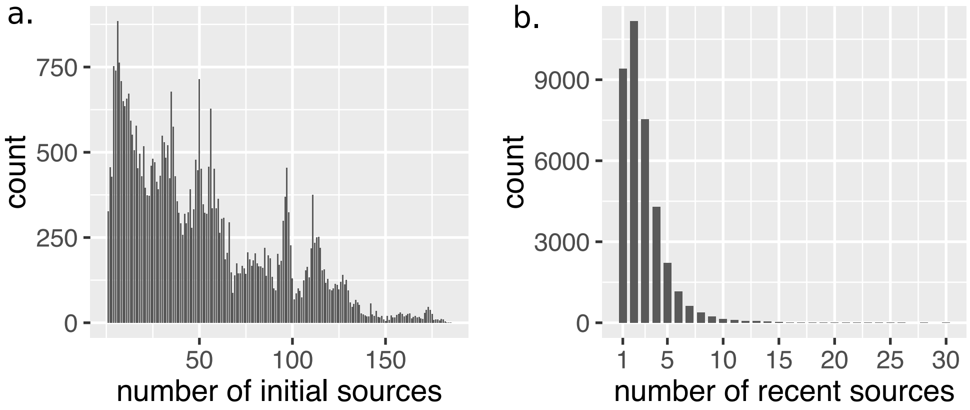


Figure 3.11 – (a) number of initial sources and (b) number of recent sources for all the entries in all contests

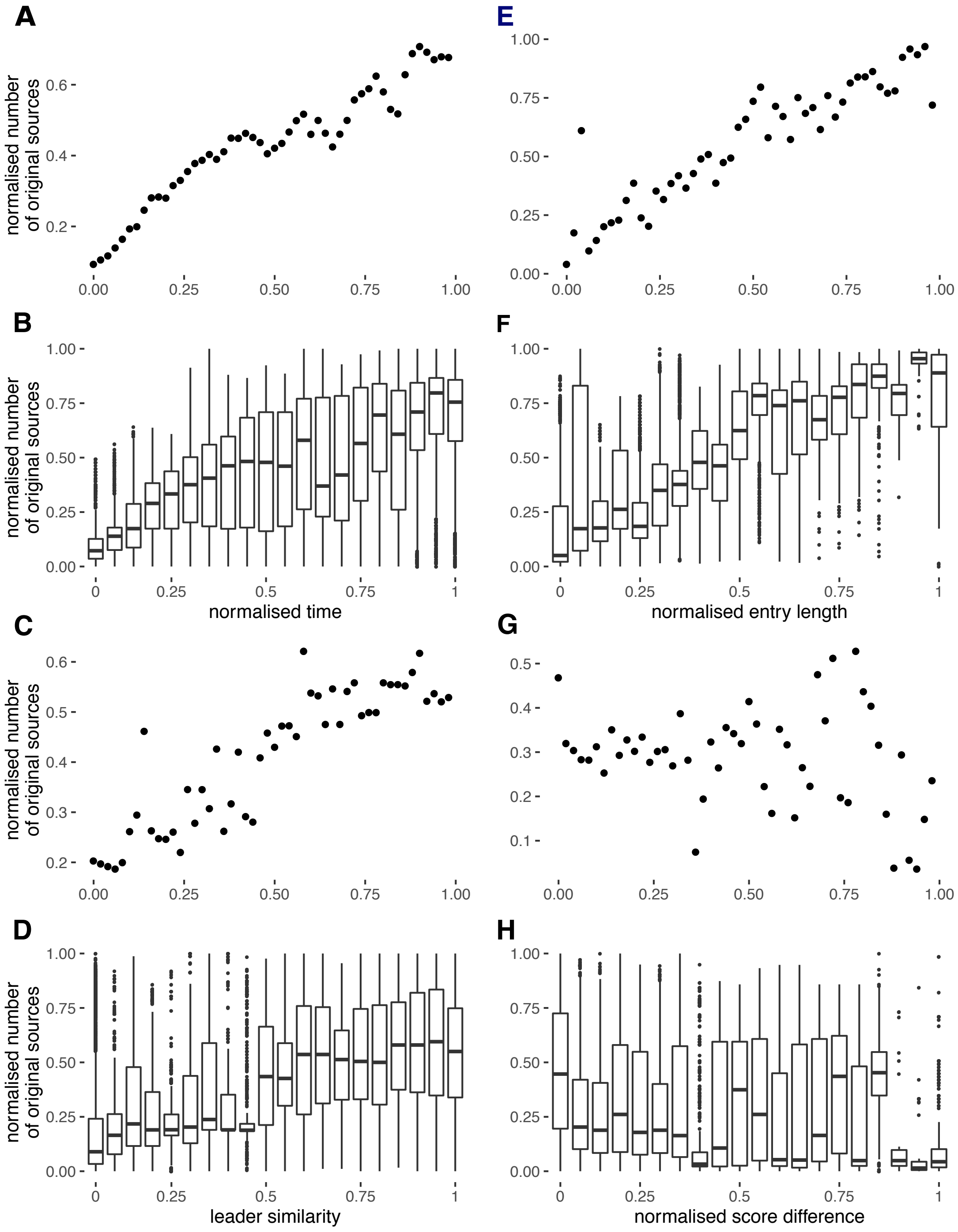


Figure 3.12 – Normalised number of original sources for all entries as a function of (A, B) time, (C, D) similarity to the current leader, (E, F) entry length and (G, H) score difference to the current leader. For ease of visualization, each of the four variables has been split into bins, and for each bin we have calculated the average number of original sources (A, C, E, G – over 50 bins), and we are plotting the distribution of the number of original sources in that bin below (B,

3.4. Discussion

I have shown that cumulative cultural evolution in the microcosms of the MATLAB programming contests is driven by high levels of cultural transmission with a strong payoff bias. Even though copying is associated with smaller performance increments, it is also associated with a much lower risk of significant performance decreases. The result of this dynamic is population-level homogeneity in behaviour, with simultaneous production of ratcheted improvements in performance.

When trying to advance in such a difficult task where improvements become very challenging very quickly, copying pays off or, perhaps more accurately, not copying can incur significant costs on performance. The optimal choice is to resort to copying the current leader, and this is what most participants do, as illustrated by the similarity and diversity dynamics throughout the contests. As a result, the population moves from a large diversity of solutions to all converging on virtually the same behaviour, which gives rise to population-level patterns comparable to expectations under conformist bias at the individual level.

The MATLAB programming competition provides a very realistic model of real-world technological evolution in a confined population, which allows the experimental study of cumulative culture on a scale that has never been attempted before. Like real human culture, it involves a complex optimisation task that allows for the open-ended evolution of solutions, which vary on several dimensions. Unlike previous experimental studies of cumulative culture that require participants to copy a model, here solutions can vary without limit, within the constraints of the programming language. A solution can be copied because it is more effective, more interesting, faster, clearer to understand, or has been submitted by a prestigious individual. Admittedly, there is no direct social interaction, but individuals interact through their solutions, and can freely copy according to no pre-specified rules. This freedom in both artefact design and social learning choice means this is a very general model for studying cumulative culture.

Ironically, this freedom also serves as the biggest drawback to this framework. Because individuals have full access to all information regarding the entries, they can also see each entry's exact score. Arguably, in many ecologically valid situations, cumulative culture involves no direct information regarding the payoff of a behaviour or artefact. In this sense, the MATLAB contest models a subset of cumulative cultural evolution that involves relative transparency – while the artefacts themselves are complex and require expert knowledge in order to understand, the outcomes can be straightforwardly judged.

Payoff bias, or copying the best performing individual, is crucial for explaining these results. Direct access to scores allows participants to judge the worth of strategies at minimal cost. Convergence here relies on accurate knowledge about payoffs, and with less precise knowledge this pattern might break down (although the same convergence could be supported by a different mechanism, like model bias for example, which allows individuals to choose who they copy from based on the characteristics of the model). This reliance on payoff bias restricts the search space and makes it more manageable within the vast solution spaces of the computer coding tasks, which would be impossible to fully explore given the time constraints of the contest.

It is important to note that this convergence dynamic does not necessarily mean that the population is converging on the globally best solution. As an individual, it makes sense to capitalise on the investment that other individuals in a population have already made in developing the current best solution, but this could result in populations ignoring and therefore failing to realise the potential of new innovations if they are not immediately the best solution. Instead, individuals pursue the current consensus largely because of the effort that has already been put into it – creating the potential for a cultural version of the 'Concorde fallacy' (Dawkins and Carlisle, 1976). Once a population has scaled a particular peak in the solution landscape, ideas that are introduced later do not get the same opportunity to climb to that altitude if they do not immediately better the current leader.

It has been argued that recombination of different ideas is a major driving factor in cumulative culture (Boyd, Richerson and Henrich, 2011a), but the concept remains vague and the evidence scarce. Here I conceptualise it as a spectrum spanning the combination of different sources, either original innovators or recent exploiters, and show that although most solutions are based on a very small number of sources as a results of copying, the population as a whole draws on an increasing number of initial sources, which persist over time. This sheds little light on the individual mechanisms involving recombination, but I expect that focusing on the best solution restricts the search space, and might also limit how many combinatorial elements are identified, which would limit recombination.

The recombinatorial aspect of cumulative culture relies on correctly identifying effective elements in different solutions and successfully incorporating them in a new solution. This is a time consuming task, and, crucially, the effectiveness of these separate elements is not necessarily correlated with the effectiveness of the overall solution. I have shown that participants consistently focus their efforts on the best solutions, and this not only restricts their search space, but might also limit how many elements with potential use in recombination are inspected, which could explain the patterns we observe. It is possible that relaxing time constraints in the contests could result in more recombination activity.

The spectrum between pure innovation and pure copying in this context is very wide and difficult to carve up into useful concepts and, naturally, the interpretation of these results in light of the issue of recombination will depend on our definitions. Here I chose to call innovation the introduction of any new code to the contest, and restrict recombination to those cases in which individuals combine information already existing in the contest. An alternative conceptualisation of these phenomena would shift these thresholds such that recombination would cover any combination of new and old information, while innovation would purely refer to entirely new code. However, this view would provide little use in the context of the programming competition, as virtually no entry is entirely new according to our line-based measure, and would mean that all entries fall into the recombination category, with a large variation in the number of sources entries draw on. Intuitively, though, the introduction of novel information hints at innovation –

modification is, after all, a type of innovation – which is why this work focuses on a narrow view of recombination of information already established in the population.

Similarly, there was a continuous spectrum in terms of social learning between pure innovation and pure copying in the context of the programming competition. I have shown that the distribution of similarity to the current leader shows both that copying took place at a high rate in all contests, and that there were also ‘maverick’ entries, very different to the current best solution, indicating attempts at complete or radical innovation. This result is in line with work by Efferson et al. (2008) who, in an experimental study of conformity that allowed participants to choose to copy each other in a two-armed bandit task, found that participants showed individual differences in their preference for social learning. While most participants did indeed conform, and self-reported as social learners, a small minority refused to make use of social information. I found the same pattern in the code similarity to the current leader, but as there is no obvious point on the innovation/copying spectrum that cleanly splits the entries into copiers and mavericks, I analysed copying on a continuous dimension. I return to this question with a full exploration of individual differences in Chapter 4.

These results are related to the issue of conformity, which has attracted significant attention in the cultural evolution field because it underpins Boyd and Richerson’s (1985) cultural group selection theory for the evolution of cooperation. These authors have used theoretical models to suggest that conformist bias should be favoured whenever social learning is favoured, but the extent to which humans or non-human animals show conformist bias in their social learning is subject to debate (Eriksson and Coultas, 2009; Morgan and Laland, 2012; van Leeuwen and Haun, 2014). Importantly, much of this body of research assumes homogeneity of behaviour at the population level is a result of individual-level tendencies to copy the majority, but we question whether this assumption is always necessary for the cultural group selection theory to hold.

Chudek and Henrich (2011) emphasise the interaction between cumulative culture and conformity in a gene-culture coevolution explanation of large-scale human cooperation. According to these authors, cumulative culture sparked a series of cognitive adaptations for improved social learning and coordination (which include conformist transmission) that they term norm-psychology. These norm-psychology processes support cooperation, which spreads through group selection, which in turn increases selection for prosocial norm-adherence. They assume that cumulative culture gives rise to a cognitive tendency to copy the majority, which becomes an integral part of norm-psychology. My analysis implies that once early human culture became cumulative, it might have resulted in patterns of convergence in behaviour without the need for an individual conformist bias by the same mechanism we observe in the programming contests. Behavioural homogeneity could result from independent individual decisions based on payoff bias in a cumulative cultural context, through mechanisms we have illustrated here. Similarly, behavioural homogeneity could also be a result of local adaptation of other types of learning biases like payoff bias, which would lead the population to converge on a uniform set of cultural traits, thus supporting the fact that conformist transmission is not necessary for behavioural homogeneity.

In a cumulative setting where high-fidelity learning is common (potentially through material artefacts – here, cultural transmission was materially supported as individuals could copy and paste code directly), and tasks reach sufficient complexity that the differential risks of copying versus innovation we have observed here are established, convergence in behaviour at the population level is expected. Although this convergence is not initially driven by conformist bias, it could then feed back to select for conformist bias and norm-conformity because, as our results show, cumulative culture makes copying a low-risk option. This would support Chudek and Henrich's suggestion that the evolution of cumulative culture and conformity are intimately linked.

This chapter raises interesting questions regarding the optimal way of achieving collective improvements. Previous work has shown that novelty in science is risky, but can be associated with considerably higher long-term impact (Wang, Veugelers and Stephan, 2016). Our data show multiple examples of populations persisting with a style of solution that ultimately proves to be sub-optimal relative to those submitted later. If the emphasis on copying we see is driving the population to persist in suboptimal behaviours, essentially for fear of losing the advantages from the investment already present in the current best solution, is this actually the optimal way to ratchet cumulative cultural solutions? The answer to this question could have important implications for organizing efforts to collectively overcome challenges: should we concentrate resources on the current leaders, implying progress will be incremental and possibly overlooking revolutionary innovations, or should we actively seek diversity to encourage innovation, accepting the risk that only few ideas will be successful? I suggest that the nature of the relationship between innovation and cumulative cultural evolution therefore merits further investigation.

Chapter 4

Individual Variation and Cumulative Culture

Abstract

Recent experimental work has identified stable individual differences in the use of social learning, which are consistent cross-context, but no investigation of individual differences in a cumulative cultural context has been attempted yet. Here I used the data from the MATLAB competition to explore individual differences in performance and the use of social information, as well as answer questions about how individuals are copied, and how the variation in participant make-up affects cumulative improvement cross-contest. I found considerable variation both between and within individuals. The cumulative setting and its associated tweaking behaviour allowed individuals to improve solutions without considerable effort, but overall better performance was associated with more investment in solutions. While there was no clear split between copiers and innovators, better players showed more variation and more exploratory behaviour in terms of novelty of solutions. Additionally, I found that the individuals formed 'reputations' within and across contests, which affected how entries were copied, consistent with prestige-type effects. Finally, I found no effect of population size, or participant composition, on improvement at the contest level.

4.1. Introduction

The previous two chapters have discussed cumulative culture in the context of two different methodological approaches leading to encouragingly similar results centred on a loss of cultural diversity associated with cumulative cultural improvements. This chapter will explore the issue of diversity at the individual level, answering questions about whether individual behaviour is variable with respect to social learning in a cumulative setting, and whether this variability affects improvement.

Individual differences in a population are intrinsically essential for natural selection to operate on, but the growing field of animal 'personality' has brought into focus the existence of not only variation, but consistent, stable individual differences between individuals across contexts (Sih, Bell and Johnson, 2004; Thornton and Lukas, 2012; Roche, Careau and Binning, 2016). In the context of social learning, 'personality' traits such as exploratory behaviour seem to lead to stable individual differences in social information use, but these differences have also been shown to be the result of developmental cues, physiological condition, or past experience (Mesoudi *et al.*, 2016). For example, pregnant ninespine sticklebacks show more social learning than non-pregnant females, potentially because social learning is safer in terms of predation risk, which pregnant females are more vulnerable to (Webster and Laland, 2011). Finally, humans seem to show evidence of cultural variation in social learning, suggesting that social learning biases can themselves be learned socially (Heyes, 2012a). This suggests that individual differences in social information use might be subject to high phenotypic plasticity, thus providing a mechanism for fast environmental adaptation (Mesoudi *et al.*, 2016).

Nonetheless, while there is experimental evidence for cultural differences in social learning between societies that differ in their individualist – collectivist tendencies for instance (Mesoudi *et al.*, 2015), little systematic work has tried to go beyond identifying and describing these differences to try to understand what causes them. Indeed, much of the modelling work, for example, has been concerned with identifying the adaptive value of social learning and culture by investigating the conditions under which social learning is more beneficial than individual learning simply by framing individual differences in terms of pure individual learners and pure social learners. For instance, earlier work usually assumes individuals have fixed strategies – either exclusively individual learners or exclusively social learners. In such a context, under a changing environment, neither phenotype wins (Rogers, 1988).

Subsequent work on Rogers' paradox has shown that culture becomes adaptive once individuals are allowed to employ strategies selectively (Enquist and Eriksson, 2007) and this work has been confirmed experimentally (Kameda and Nakanishi, 2003). Since then, a large body of theoretical and experimental work has shown that individuals use either social or asocial learning flexibly depending on the context. For example, both humans and non-human animals rely on social learning more when they are unsure of the payoffs (Kendal *et al.*, 2005; Galef, Dudley and Whiskin, 2008; Morgan *et al.*, 2012; Toelch *et al.*, 2013).

Additional to this evidence for individual flexibility across contexts, more recent findings on human culture have shown consistent differences in the individual predilection to use either social or asocial information in decision-making. A study looking at conformity using both theoretical and experimental approaches found that, in a two-choice experiment in which they were given an option to socially learn, participants split into 'conformists', as expected from a rational player, and 'mavericks', who refuse to access social information even though it would have been to their advantage (Efferson *et al.*, 2008). These personal preferences have been confirmed by further studies that found individual differences in social learning strategies (Mesoudi, 2011a; Molleman, van den Berg and Weissing, 2014), and consistent individual differences in participants' propensity to use social learning across contexts (Toelch *et al.*, 2013).

This finding regarding the prevalence of individual differences in social information use, arising somewhat unexpectedly in the process of investigating social learning strategies, has profound implications for the way we conceptualise and model social learning, making it clear that accounts of cultural evolution assuming homogenous populations are neither realistic nor complete. To my knowledge, though, no work has purposefully explored individual differences in a cumulative cultural evolution setting, which is what I set out to do in this chapter. Thus, the first focus of this chapter will be investigating whether there are consistent and distinct individual strategies in social learning use in a cumulative setting, and whether these strategies are linked to performance.

Finding individual differences in social learning and performance in a cumulative setting would raise questions regarding whether these differences affect how individuals behave as cultural learning models. For example, in populations with a complex cultural repertoire, where the link between a cultural trait and its payoff is opaque, individuals need to find effective heuristics to guide their social learning. Prestige, defined as high status or influence typically related to good performance and age, arising from complex social exchanges, can be such a heuristic (Henrich and Gil-White, 2001), and there is real-world evidence that people indeed use it. For example, Fijian villagers show evidence of a predilection to learn from more successful or more knowledgeable individuals (Henrich and Broesch, 2011). Importantly, this preference extends across domains – for example, being perceived as a successful yam grower would still increase the probability that an individual's fishing techniques would be copied – and it is precisely this cross-domain influence that is indicative of prestige bias in social transmission. Prestigious individuals are not just successful at fishing, for example, but gain this prestige from multiple interactions across different contexts and domains.

The complex interactions characterising cumulative culture provide an ideal context for prestige bias to emerge. Although I have shown that payoff bias is an easy, accessible rule even in a cumulative cultural setting (Chapter 3), and indeed seems to be a preferred strategy when available (Mesoudi, 2011a), it is of interest to see if this copying rule is exclusively used or whether individual differences in a cumulative setting generate reputations that are used as a guide for social learning. Thus, the question of whether prestige-like processes emerge from the individual variation witnessed in a cumulative setting represents the second focus of this chapter.

Finally, there is compelling evidence that the individual make-up of a population will affect the accumulation of improvement in that population. As discussed in Chapter 1, a large body of work has addressed the relationship between group size and cumulative culture, both through theoretical (Henrich, 2004; Powell, Shennan and Thomas, 2009) and experimental approaches (Caldwell and Millen, 2010; Derex *et al.*, 2013; Muthukrishna *et al.*, 2013). The experimental approaches in particular suffer from the methodological limitations surrounding sample sizes and task complexity discussed in Chapter 3. For example, modelling and field studies interested in the relationship between population size and cumulative culture involve group sizes in the thousands (Kline and Boyd, 2010), while experimental studies usually involve groups of 3 or 5 individuals – the largest group size investigated experimentally did not exceed, to our knowledge, 16 participants (Derex *et al.*, 2013).

A recent study purposefully framed the group size issue regarding cumulative culture in terms of mitigating loss of skill rather than promoting skill accumulation (Muthukrishna *et al.*, 2013). This study contrasted social learning in a cumulative setting in two conditions involving either one or 5 models, finding that individuals allowed to observe 5 models show better skill preservation over time. It is, however, unclear whether results obtained under this type of methodology extend to cultural accumulation in populations comprising thousands of individuals or whether they tackle learning from multiple sources of information, rather than incremental improvement. Indeed, recent theory suggesting that the effect of population size on cultural accumulation becomes less important the more populations grow points in this direction (Andersson and Törnberg, 2016).

Additionally, work on individual differences in human social learning has shown that individual variation in learning strategies can promote the spread of beneficial behaviours, and populations characterised by individual variation may be more successful . The authors showed that an effective solution spreads faster in a population where individuals employ either payoff bias or frequency-based learning, than in a homogenous population in which all individuals equally use both types of learning (Molleman, van den Berg and

Weissing, 2014). The final question addressed in this chapter is therefore the nature of the relationship between group size, individual variation, and cumulative improvement, in a larger sample size of typically 100 participants, using a complex cumulative task.

In this chapter I used data from the MATLAB competition introduced in the previous chapter to answer a number of questions about how variation affects performance at the individual level, whether this variation promotes prestige-like effects in a cumulative setting, and whether group size and variation affect improvement across contests. Specifically, is there considerable within-individual variation in copying or can individuals be classified as 'copiers' and 'mavericks' (Efferson et al., 2008)? How are improvements in the contest related to individual social learning use, both at the individual and the group level? Do individual characteristics lead to the formation of so-called 'reputations' within and between contests, which affect how individuals are copied? Does variation across contests in individual strategies relate to improvement?

The first section of this chapter will address the first two questions, characterising individual variation in terms of activity, performance, and social information use, and linking this variation to improvement at the individual level. The second section will investigate whether individual characteristics of performance lead to prestige-like effects that affect copying within and between contests. Finally, the last section will be concerned with whether improvement at the contest level is a matter of population size or, rather, whether the characteristics of specific individuals in the population are better predictors of cultural accumulation.

4.2. Methods

This chapter uses the same dataset as Chapter 3, originating from a series of 19 online competitions organised by MathWorks. As discussed in Chapter 3, throughout the week of each contest, participants were allowed to submit as many solutions as they wanted, which resulted in numerous participants submitting multiple entries. The participants were identified using an identification number that was linked to a MathWorks account, which they themselves created and which was needed to submit entries to the contest. Individuals were not forbidden from creating multiple accounts if they wished to do so, but I have reason to believe, based on online communication between participants, that most did not. Additionally, since this would have required substantial effort (e.g. creating a new account, linked to a new email address), I expect this was not a major confounding factor in this analysis. Nonetheless, because there was no means of identifying such potential repeat participants, the analysis presented in this chapter does not attempt to engage with the issue of single participants submitting from multiple accounts. When quantifying the number of unique participants in a contest, for example, I assume no overlap.

Overall, our sample included 2,645 participants from 19 contests, and a total of 56,663 entries. Participants submitted an average of 21 entries each, but with very large variation between participants, ranging between 1 and 1,502 entries each. This repeated submission framework allows us to define a distribution of entries for each participant and use it to characterise variation both between and within individual participants, to assess within- and between-individual correlations, as well as to relate these correlations to cross-contest variation in performance.

In this chapter, I characterised this individual variation through three principal metrics that I term activity, performance, and novelty. Activity (the number of entries submitted) at the individual level is an indirect measure of motivation – we expected that more motivated, more interested players would submit more entries throughout the contest. Novelty, measured as the proportion of novel lines of code, is evidently linked to social learning –

copying in the context of the MATLAB contests constitutes social learning – and this measure allowed us to quantify and investigate individual differences in social learning. Finally, performance in the contest in terms of score and improvement in score was a measure of both individual and collective improvement in task.

For the rest of this chapter, I have grouped entries according to the participant that has submitted them (henceforth called 'author') within each contest. Each author is responsible for a collection of entries, which can be characterised in terms of activity, novelty, and performance, and which define the 'strategy' of that player in the contest. The analysis in this chapter includes only valid entries, which followed the contest guidelines and received a score. Although it is the case that several participants have taken place in multiple contests, we are mainly interested in within-contest dynamics (how individuals vary in their solutions, their copying, and their performance). Because each contest presents a different challenge, it would be less useful to investigate the variation in solutions across contests within one individual, because this variation is very likely to be intrinsically linked to the space of possible solutions each challenge provides. Therefore, I treat each contest as independent, and do not take into account repeated participation, nor try to link identities across contests. Section 3.2.1. provides the only exception to this convention, where I specifically investigate variation within individuals who participated in multiple contests.

4.2.1. Individual variation

Chapter 3 discussed in detail the patterns of convergence emerging throughout the contest as a result of considerable copying. The overall novelty, defined as the proportion of new lines each entry introduces to the contest, decreases drastically over time, and the similarity to the current leader experiences a sharp increase as soon as participants are allowed to see each other on day 3 of the contests (Fig. 4.1). In this section I investigated novelty at the individual level and how participants employed novelty in their entries as part of their individual strategy. This allows us to establish whether we see a consistent split into 'copiers' and 'mavericks' or whether individuals submit a wide range of entries varying in their novelty content, as well as whether consistent social learning strategies affect performance at the individual level.

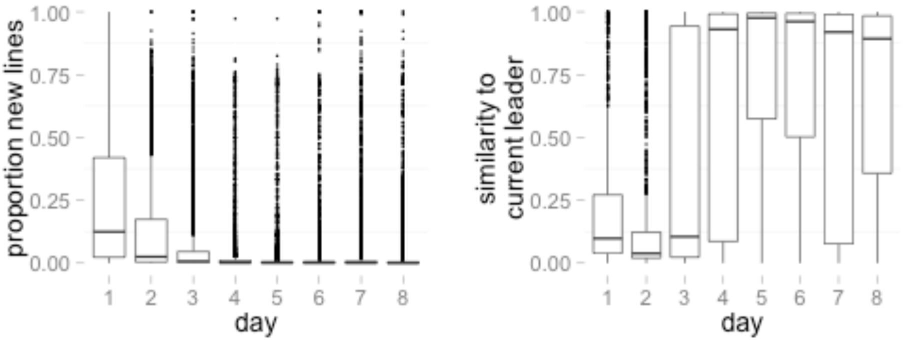


Figure 4.1 – proportion of new lines and similarity to the current leader for all passed entries in all the contests, over time.

For each participant, I used two measures of novelty. One is the proportion of lines novel to the contest in each entry (calculated as the number of new lines in an entry, over the total number of lines of that entry), an absolute measure of novelty. Since I have shown in Chapter 3 that extensive copying of the current best entry takes place, I also used the similarity to the current leader as a second, relative measure of novelty. As in Chapter 3, the code similarity was measured using the Czekanowski similarity, given by:

$$CZ_{ik} = 2\,\frac{\sum_{j=1}^{S} \min\,(x_{ij}, x_{kj})}{\sum_{j=1}^{S} (x_{ij} + x_{kj})} \quad \text{(Equation 4.1)}$$

where CZ_{ik} is the similarity between samples i and k, x_{ij} is the number of instances of species j in sample i, and x_{kj} is the number of instances of species j in sample k. For our analysis, each sample corresponds to an entry, and each species is a line of code. Every entry is a set of lines of code, so the similarity between two entries is a function of the total number of lines they have in common, including reoccurring lines, relative to the sum of their lengths.

As each individual was responsible for submitting a collection of entries that could be characterised both in terms of the proportion of novel lines and the similarity to the current leader, each individual could thus be characterised by a distribution of the proportion of novelty of his or her entries, and a distribution of leader similarity. Here I explored these distributions to establish whether individuals can be distinctly classified in terms of ‘copiers’ and ‘mavericks’.

In order to quantify performance, an entry’s score would be an obvious measure, but score improves steadily, and improvements become increasingly difficult throughout the contest, so an improvement in score at the beginning of the contest is not comparable to a similar magnitude improvement in score at the end of the contest. I used score difference between each entry and the current leading entry as a continuous, relative measure of performance, which takes into account the continuous improvement in score.

The score of the leading entry at each time point represents the best performance at that time, and the overwhelming majority of entries score worse than the current leader (i.e. very few entries take the lead overall; Chapter 3). Since a decrease in score represents an improvement in performance, then the score difference between the score of an entry and the score of the current leader will be negative for entries that improve the overall score, and positive for most entries – a bigger difference would indicate a particularly unsuccessful entry. In order to make interpretation easier and more intuitive, I reversed the signs of these score differences. Therefore, a positive increment represents an improvement to the overall score – the higher the increment, the higher the improvement – and a negative increment represents a worse performing entry relative to the current best – the lower the negative value, the worse the performance. In order to reliably compare these values across contests, I rescaled this increment within each contest so it falls between 0 and 1 (while maintaining the sign, either positive or negative), following:

$$I' = \frac{I - I_{min}}{I_{max} - I_{min}} \text{ (Equation 4.2)}$$

I tested whether novelty is associated with performance at the individual level, using non-parametric Spearman correlations as the data were not normally distributed.

Alternatively, a more straightforward measure of performance is whether an entry becomes a leader (i.e. achieves the best score at the time of its submission and thus improves the overall score). Extending this to the author level allows us to quantify how many of each author's entries improved upon the current leader. Here I split participants into leading authors (i.e. authors who submit at least one leading entry that beats the current best in the entire contest), and non-leading authors. By focusing on the differences between these two groups, we can investigate whether successful authors use novelty differently.

Leading authors are particular because they have submitted both entries that score worse and entries that score better than the current leader. Therefore we can distinguish between positive score differences (i.e. score improvements), which correspond to the entries that scored better than the current leader, and negative score differences, which correspond to those entries that scored worse than the current leader. Thus I answered questions about the relative magnitudes of these positive and negative score differences, and whether leading and non-leading authors differ in their overall performance.

To test the difference in performance between leading and non-leading authors, I fitted a linear mixed model with each entry's score increment relative to the current leader as the dependent variable and a fixed factor as independent variable that specifies whether an entry 1) was submitted by a leading author and makes a positive contribution to the current leader score (i.e. is an overall improvement), 2) was submitted by a leading author but does not improve the overall score, or 3) was submitted by a non-leading author, and therefore does not improve the overall score. Setting condition 2) as the baseline allows testing whether there was a difference in magnitude between positive and negative increments within leading authors by comparing conditions 1 and 2 (are improvements bigger than decreases in score in leading authors?). This also allows to test whether there was a difference in negative increments between leading and non-leading authors by comparing conditions 2 and 3 (are leading authors better than non-leading authors even in those entries that do not take the lead?). In order to control for the fact that improvements might differ in difficulty and, therefore, magnitude between contests, the model included contest as a random effect. Moreover, to control for the fact that some individuals are inherently more skilled independent of their leader status, the model also included author as a random effect, nested within contest.

Finally, I used non-parametric Wilcoxon tests to establish whether there were differences in the average use of novelty and in exploratory behaviour between leading and non-leading authors.

4.2.2. Influence

Here I investigated whether individuals formed reputations within and across contests, and whether those reputations affected how the individuals were copied. This links with Henrich and Gil-White's notion of prestige (Henrich and Gil-White, 2001), and although the MATLAB does not allow for direct interaction between participants, it does allow testing hypotheses proposed by the authors like whether people preferentially copy successful individuals, and whether prestigious individuals are influential even beyond their domain of expertise. I expect the MATLAB contests will bring positive evidence for both those hypotheses. In order to test this I define 'prestige' or prestige-like effects in terms of whether individuals manage to take the lead, i.e. achieve the best score at the time of an entry's submission. This is a remarkably salient signal, as the top of the leaderboard was closely monitored throughout each contest, and I expect that individuals who managed to take the lead should have higher influence on subsequent entries. Even more, this framework allows testing whether this influence carries across contests, a proxy for different domains – surely, MATLAB expertise is required for success in this context across all contests, but whether individuals should be expected to perform just as well on different problems remains an empirical question.

Chapter 3 showed evidence of a strong payoff bias in the MATLAB contests, as the current best entry at any time seems to be preferentially copied. In this chapter I investigated whether this effect extends at the individual level and whether individuals recognise leading authors as more successful and use this recognition to guide their copying. Moreover, in previous analyses each contest was treated independently, but it is the case that the same individuals participated in more than one contest. Thus it was possible to investigate whether individual participants formed cross-contest reputations and whether reputations affected the way they were copied. If leading authors showed more influence irrespective of how well their entries score, this would be evidence of a prestige-type effect. If the effect held cross-contests, and leading authors had more impact if they had also been leading authors in previous contests, for instance, then the evidence for prestige bias would be even more convincing.

4.2.2.1. Influence measure

To this end, I needed to establish the extent to which an individual was copied throughout the contest. This was challenging since there was no unambiguous record of whether an entrant was copying a specific individual at the time they submitted their entry. The closest proxy for copying used so far is the similarity between two entries: if the similarity between an earlier and a later entry is high enough, more often than not the later entry copied the earlier one to some extent. This does not exclude, however, the possibility that the two entries are related through copying via a third entry. Instead of attempting to quantify how many entries a submission has been copied by, I devised a measure I call 'influence' that attempts to capture how much of an entry the population has picked up following the entry's submission.

Influence is a continuous population-level measure of subsequent similarity that indicates how a given solution, once introduced, persists in the population. This measure does to some extent distinguish between the initial innovator and the following copiers, but it does not completely discount copiers. We would not want to ignore the fact that although an initial innovator introduces an idea in the population, it could be that a subsequent copier manages to popularise it - in a way, copiers have as much influence as the initial innovator if they were clever enough to copy a successful solution.

More specifically, influence was calculated as the average similarity between an entry and all subsequent entries. The influence of the entries submitted at the beginning of the contest will naturally be lower than the influence of the entries submitted towards the end, purely because for the entries submitted at the beginning there is a higher number of entries that could potentially diverge from them. Therefore I divided this average similarity by a serial number indicating the point along the contest timeline of the entry's submission. This number ranges between 0 and the total number of days in each contest (typically 7), with a precision of 4 decimals (such that the first entry is submitted at time 0, the second at time 0.0291 for example, etc.). Because of the difference in magnitude between similarity and this measure of time, influence is skewed, assigning very high numbers to initial entries. Therefore the analysis used a log-transformation of the influence measure. Thus, influence was given by:

$$influence = \log\left(\frac{mean\ similarity}{time} + 0.001\right) \quad \text{(Equation 4.3)}$$

Finally, this influence measure was rescaled between 0 and 1 using the same form as Equation 4.2 above, to make comparison across contests possible.

As discussed in Chapter 3, more than half of the contests consisted of three periods of visibility. In 'darkness', the first day, participants were only allowed to see their own entries and score. In the second day, 'twilight', participants could additionally see their own rankings compared to the other participants. Only from the 3rd day on, in 'daylight', did participants have full access to all the other entries and their scores. Because here we were interested in how reputations are formed once participants can see and copy each other, the influence analysis only included data from 'daylight', from the 3rd day onwards, and only included valid entries that received a score.

4.2.2.2. Statistical analysis

In order to test whether leading authors had a higher influence than non-leading authors both in their leading and non-leading entries, I fitted a mixed linear model with the influence of each entry as the dependent variable and a factor with three levels that specified whether 1) the entry took the lead and was submitted by a leading authors, 2) the entry did not take the lead but was submitted by a leading author and 3) the entry did not take the lead and was submitted by a non-leading author. The baseline was set to group (3), the entries that did not take the lead and were submitted by non-leading authors. The model included the entry's score increment as a fixed effect to control for the fact that better performing entries might have higher influence irrespective of who submitted them. The author and the contest were included as random effects, with author nested within contest, to control for the fact that each contest might be characterised by a different average level of copying, and the fact that within each contest some authors might have generally higher influence independent of their leader status. Therefore the model specification was:

$$E(Influence_{ijk}) = \alpha + \beta_i + \gamma_{ij} + \beta_1\ Increment_k + \beta_2\ AuthorFactor_k$$

$$\beta_i \sim N(0, \sigma_1^2);\ \gamma_{ij} \sim N(0, \sigma_2^2)$$

for each entry k submitted by author j in contest i.

The predictor of interest here was the author factor. We expected leading entries submitted by leading authors to have a significantly higher influence than entries submitted by non-leading authors. If there were also a significant increase in influence in non-leading entries submitted by leading authors, compared to entries submitted by non-leading authors, this would suggest that leading authors generally have more influence, which is consistent with a prestige bias.

Some individuals participate in multiple contests, which gives us the opportunity to investigate whether individuals perform consistently across different problems or whether the variation between contest problems somehow breaks down these individual characteristics. Through a similar argument as before, if authors performed consistently across contests, and if this performance lead to the emergence of reputations that individuals can use when copying, we would expect that more ‘prestigious’ individuals would have higher influence, and that this prestige-type effect will hold across contests. This was tested using a similar mixed linear model as for within-contest influence.

In this context, because authors participated in more than one contest, we could distinguish between whether the author submitting each entry managed to become a leading author in the same contest the entry was submitted in, or whether the individual managed to become a leading author in a separate contest. The predictor of interest was therefore a factor that specified whether the entry took the lead, the author submitting the entry was a leader in the same contest the entry was part of, or the author was a leader in a different contest. This factor had 6 levels: 1) non-leading entry submitted by a non-leading author who was not a leading author in a different contest, 2) non-leading entry submitted by a non-leading author who was a leading author in a different contest, 3) non-leading entry submitted by a leading author who was not a leading author in a separate contest, 4) non-leading entry submitted by a leading author who was also a leader in a different contest, 5) leading entry submitted by a leading author who was not a leader in a different contest, and 6) leading entry submitted by a leading author who was also a leading author in a different contest. As before, I included score increment as a fixed factor, and contest and author identity as random factors.

This allowed us to establish whether entries had more influence when submitted by a leading author, independent of how well they scored. Crucially, this analysis also allowed us to establish if entries had more influence when submitted by an author that was a leader in a different contest (i.e. if reputations carry across contests). If entries that do not take the lead, submitted by authors who do not become leaders in the same contest, but who had been leading authors in a different contest still have higher influence than entries submitted by non-leading authors both within and across contests, it would mean that the leadership reputation at the individual level was maintained across contests, evidence of cross-domain prestige bias.

4.2.3. Cross-contest improvement

This section addresses the question of whether improvement at the contest level can be best predicted using population size or the composition of individuals participating in a contest. In other words, is score improvement driven by "collective brain" effects or the presence of particularly talented individuals. Choosing a measure of improvement is challenging, because contests vary in the problems proposed, and because each contest allows for open-ended improvement in task.

A straightforward measure of the overall improvement in each contest is how much the entire population improves over an initial baseline score. Because each contest proposed a different challenge, and the score was intrinsically linked to the challenge, as it was a function of the algorithmic result of that problem, this overall improvement needed to be normalised by a number that characterises the problem. Fortunately, in each contest, the organisers provided a sample entry that participants could use as an example and build on. This sample entry is the first entry, and it provides a useful baseline that can be used to compare each contest improvement. Therefore, our measure of improvement was calculated as the difference in score between the best entry (the entry with the best/lowest score in our case) and the first entry, divided by the score of the first entry. This gave a measure of overall improvement independent of the algorithmic solution of each problem.

I selected a number of key measures characterising size, activity, and performance for each contest. These measures are:

- Number of authors – how many participants each contest attracted, a measure of population size;
- Number of leading entries – this is not necessarily a measure of overall improvement in a contest; rather, it characterises how incremental improvement is;
- Number of authors who took the lead – a measure of how many skilled participants there were;
- Range of mean score increments relative to the current leader per author – a measure characterising the variance in mean relative performance per author, to understand whether there is a relationship between overall improvement in a contest and how varied the performance of individuals taking part in that contest was;
- Mean leader similarity – a measure of average novelty per contest;
- Mean proportion of novel lines – absolute novelty per contest.

Does the number of authors participating in each contest relate to overall contest improvement? Or is it the case that individual make-up, in terms of how novel, variable in performance, or successful individuals are affects overall improvement? Testing the relationship between overall improvement and each of the above measures will answer this question.

4.3. Results

4.3.1. Individual variation

Individuals differed widely in their activity patterns, measured in terms of the number of entries submitted by each participant (Fig. 4.2). The number of entries per author was roughly exponentially distributed in all contests, with a very small number of authors responsible for a large number of entries, and a long tail of authors with very few entries. Indeed, 30% of authors submitted only one entry the entire contest, 60% submitted 5 or less, and less than 1% submitted more than 50 entries.

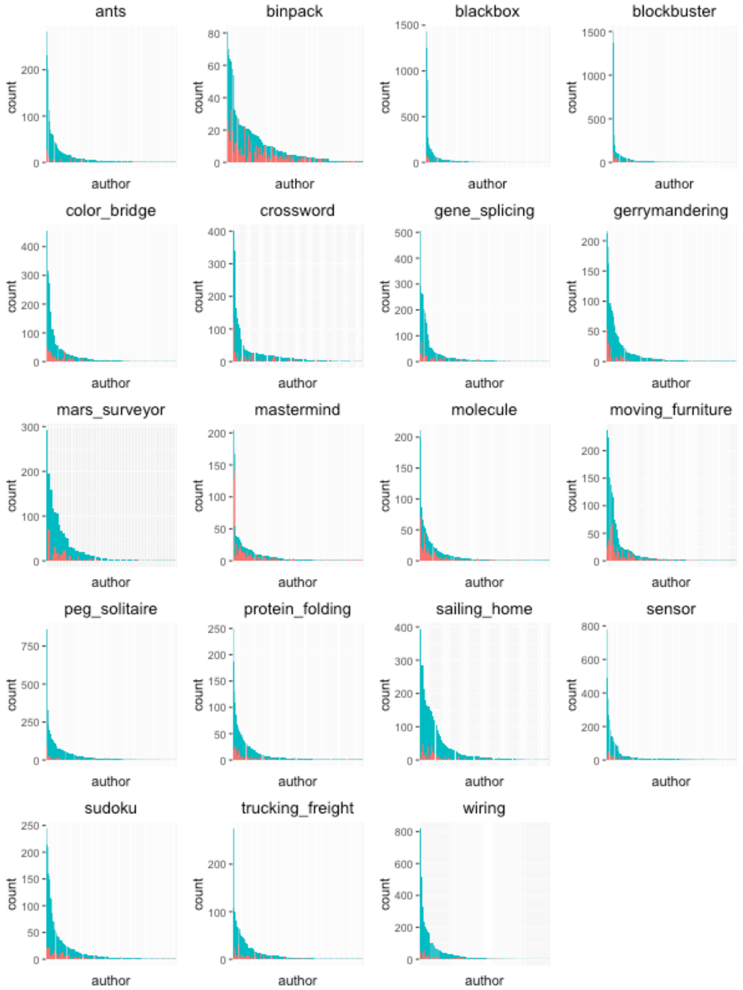


Figure 4.2 – number of total entries (red indicates failed entries, blue indicates passed entries) per author for each of the 19 contests

The distribution of leading authors was similarly skewed – a very small number of authors managed to submit at least one entry that took the lead

(Fig. 4.3a). More specifically, only 22% of all participants in all contests submitted at least one entry that took the lead, and only 14% did this more than once. This is consistent with the results from Chapter 3, which indicate that improvement in task is very difficult and most entries do not manage to take the lead.

There seems to be a link between activity and performance (Fig. 4.3b). Bearing in mind that a higher average increment indicates better average performance, while leading authors showed considerable variation in how many entries they submit, there were virtually no authors who submitted a large number of entries and performed badly. Therefore participants who were not very successful were also not very active. The variation in activity in leading authors suggests, however, that high activity is not necessary for a participant to be able to take the lead. It is perfectly possible for newcomers with no history of improvement to join the contest and beat the current best score.

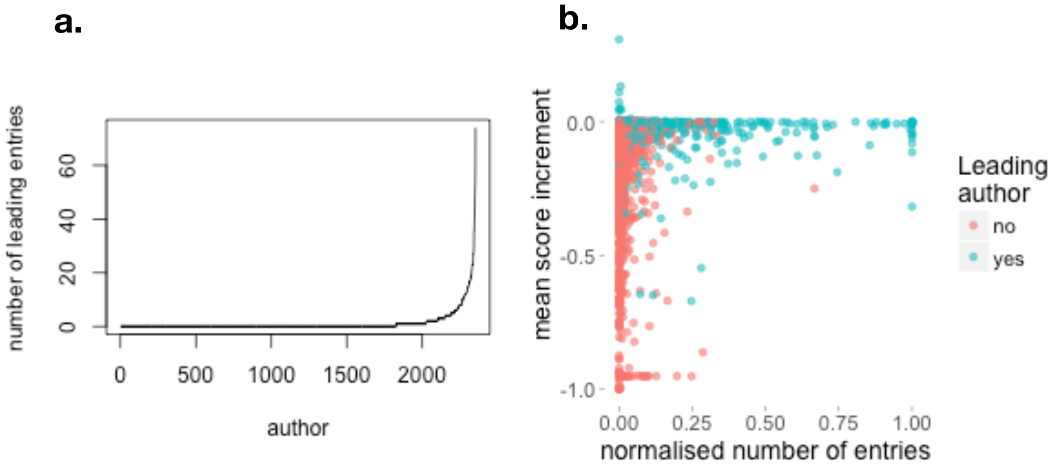


Figure 4.3 – (a) number of leading entries per author in all contests; (b) average score increment relative to the current leader, for each author in each contest, as a function of the number of entries, rescaled in [0,1]. Blue points indicate leading authors, red dots indicate non-leading authors

4.3.1.1. Novelty

Visualising the distributions for both our novelty measures (proportion of novelty and similarity to current leader) allows us to explore the average novelty introduced by an individual (i.e. whether they have a general predilection for copying), as well as the variation in that novelty (i.e. do they show consistent preferences for copying/novelty or do they exhibit a varied strategy?).

Figure 4.4a and 4.4b plot the average values per author, along with the range of each author distribution, for both similarity to the current leader and proportion of novelty. The distribution of leader similarities across authors shows a sigmoidal pattern, with more authors showing low similarity, and a relatively gradual shift from low to high average similarity. Some authors were very conservative and preferred to keep their entries ‘safe’ through copying, while some authors were relatively adventurous, submitting highly varied entries in terms of the solutions. This mirrors the pattern we saw in Chapter 3, where most entries copied the current leader and therefore scored very similarly, while some entries deviated from the code the population was currently entertaining. Therefore authors varied widely on the conservatism spectrum, but if we were to informally categorise individuals they can be broadly split into three groups: 1) a surprisingly large number of low similarity authors, ‘incurable mavericks’ who barely ever took the lead, 2) an intermediate group of ‘occasional mavericks’, who were most likely to take the lead, and 3) a smaller group of ‘extreme conservatives’ who, again, rarely took the lead.

Most leading authors and the most active authors lie towards the copying end of this spectrum, suggesting that copying is associated with better performance at the individual level. This is confirmed by Fig. 4.4c, which illustrates between and within-author variation in performance, as measured by the score increment. Most leading authors introduced small improvements on average (right-hand side of the graph), associated with more copying and less novelty.

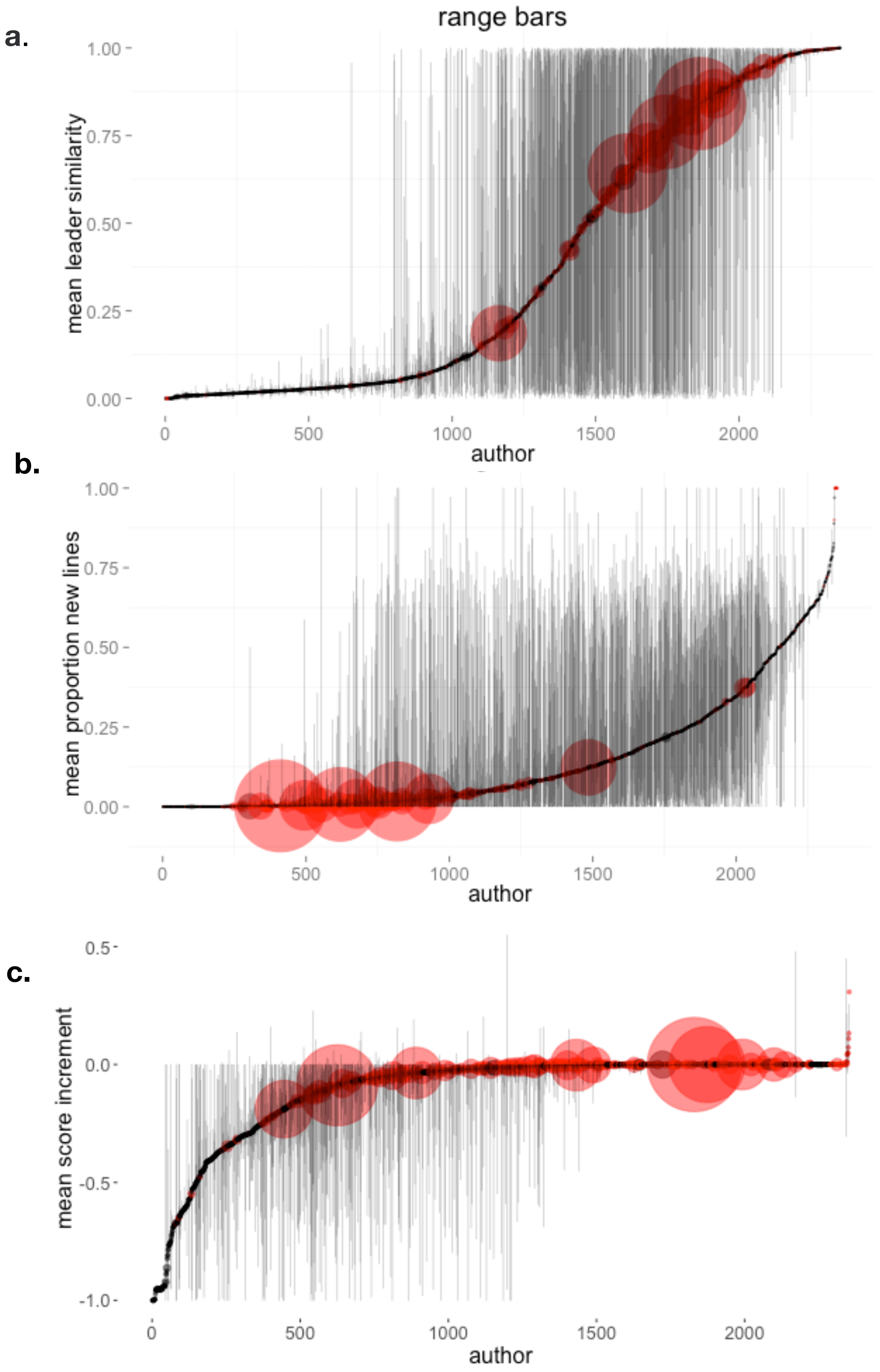


Figure 4.4 – (a) leader similarity, (b) proportion of novel lines, (c) score increment - average values with bars spanning the range of the distribution. The red points indicate leading authors (i.e. authors who submitted at least one entry that improved the overall score at the time of its submission), and the size of the points is proportional to the total number of entries submitted by each author

The majority of authors exhibited broad diversity in their entries' similarity to the current leader. Low mean-similarity authors did not seem to submit any high similarity entries (left-hand side of Fig. 4.4a), but these also tended to be authors with a small number of submissions (there was a positive correlation between the number of submissions and the similarity to the current leader at author level – Spearman $\rho = 0.22$, $p < 0.001$). Most authors however were very likely to submit both similar and dissimilar entries to the current leader, which suggests a high degree of flexibility in strategies. Very few authors limited themselves to merely copying, preferring instead to also explore solutions that deviate from the current norm. Importantly, there is no specific point on this axis that would unequivocally split authors into 'copiers' and 'mavericks' – rather, individuals fall on a continuous spectrum between absolute novelty and absolute copying, with the majority exhibiting large variation in similarity between entries.

The proportion of novel lines paints a very similar picture (Fig. 4.4b). The average proportion of novel lines per author was typically low, and more active and more successful authors tended to show a lower proportion of novelty. There was, again, a large range of variation within author in terms of novelty, which indicates individuals in this context did not split cleanly into innovators and conservatives.

Interestingly, active leading authors showed large variation in leader similarity across entries (Fig. 4.4a), but they did not show as much variation in proportion of new lines across entries (Fig. 4.4b). This is clearly illustrated by Fig. 4.5 – most authors who submitted at least one leading entry showed high values of average similarity, but low average proportion of novel lines. This, intriguingly, would suggest that while successful authors sometimes deviated from the current best, it was not because they introduced considerable novelty, but perhaps because they recombined material already present in the contest.

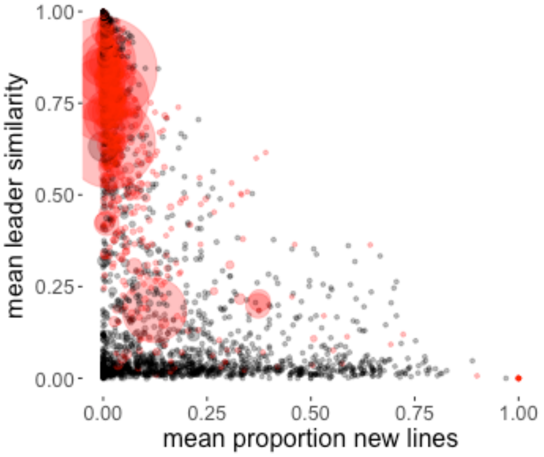


Figure 4.5 – average leader similarity as a function of average proportion of new lines, for each author in all contests. The red points indicate leading authors, and the size of the points is proportional to the number of entries submitted by each

Finally, as there does not seem to be a clear split between ‘copiers’ and ‘mavericks’, I tested whether novelty was associated with the score increment relative to the current leader. There was indeed a significant negative correlation between the average proportion of novel lines of an author and their average score increment (Spearman $\rho = -0.26$, $p < 0.001$) and a significant positive correlation between the average similarity to the current leader and the average score increment (Spearman $\rho = 0.42$, $p < 0.001$). Bearing in mind that a higher increment is indicative of good performance, this confirms that the results from Chapter 3 hold at the individual level – authors with who introduce more novelty were less successful (Fig. 4.6).

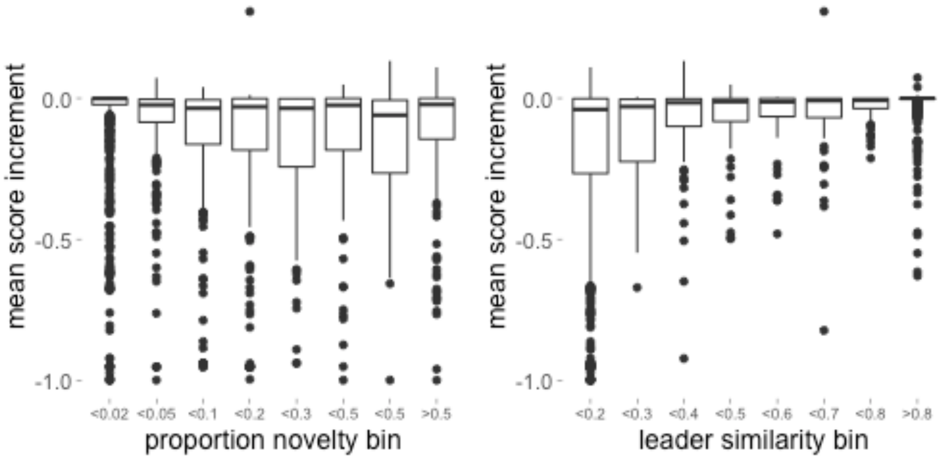


Figure 4.6 – average score increment as a function of average proportion of new lines and average leader similarity, for all authors in all contests. For ease of visualization, novelty and similarity have been grouped in bins covering approximately 10% of each measure

4.3.1.2. Leaders

The leading authors, the individuals who manage to submit at least one entry that takes the lead, represented 526 out of the total of 2353. Thus 22% of authors managed to take the lead at least once, but they were responsible for 76% of all passed entries, indicating much higher activity levels in leading authors (Fig. 4.7). The average number of entries per leading author was 10 times larger than the average number of entries per non-leading author.

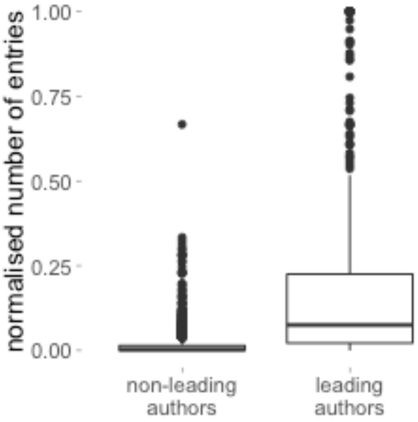


Figure 4.7 – distribution of number of entries per author, normalised over contests, for leading and non-leading authors

Figure 4.8 illustrates the difference of magnitude between positive and negative score differences within leading authors, and the results from the mixed linear model testing the differences in score increment between the three groups are presented in Table 4.1. As expected, improvements in leaders were smaller than non-successes. However, we have no reason to believe that negative score differences in leading authors should be different from negative score differences in non-leading authors, but this is precisely what the results indicate. This suggests that although there was considerable variation between individuals, leading authors performed consistently better throughout the contest than non-leading authors.

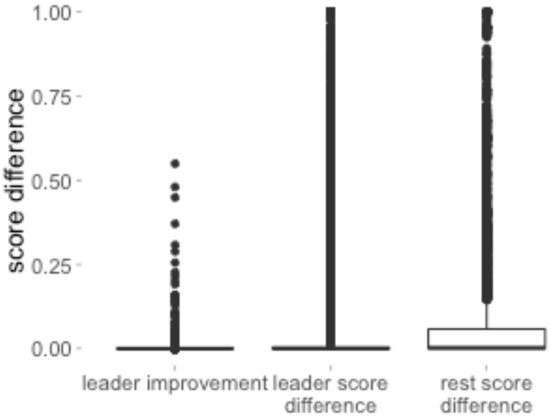


Figure 4.8 – distribution of positive score differences submitted by leading authors (left), negative score differences submitted by leading authors (centre), and negative score differences submitted by non-leading authors (right).

Leading authors also seem to be introducing novelty differently in their entries (Fig. 4.9). Non-leading authors were characterised by an s-shaped curve with higher variation concentrated around middle values, but the distribution of similarity to the current leader for leading authors displayed a relatively gradual increase in mean similarity and very wide ranges. The distributions for the proportion of novel lines did not show as much disparity, although leading authors generally displayed more variation than the rest of the participants (Fig. 4.10). This suggests that leading authors are more exploratory, deviating more from the current leading solution.

	Estimate	Std. Error	t-value	p-value
(Intercept) Leader negative score difference	**0.041**	**0.0191**	**2.08**	**0.03**
Leader improvement	**-0.029**	**0.002**	**-13.08**	**<0.001*****
Non-leader negative score difference	**0.094**	**0.008**	**11.53**	**<0.001*****

Table 4.1 – results from linear mixed model *increment ~ group + (1|contest:author)*

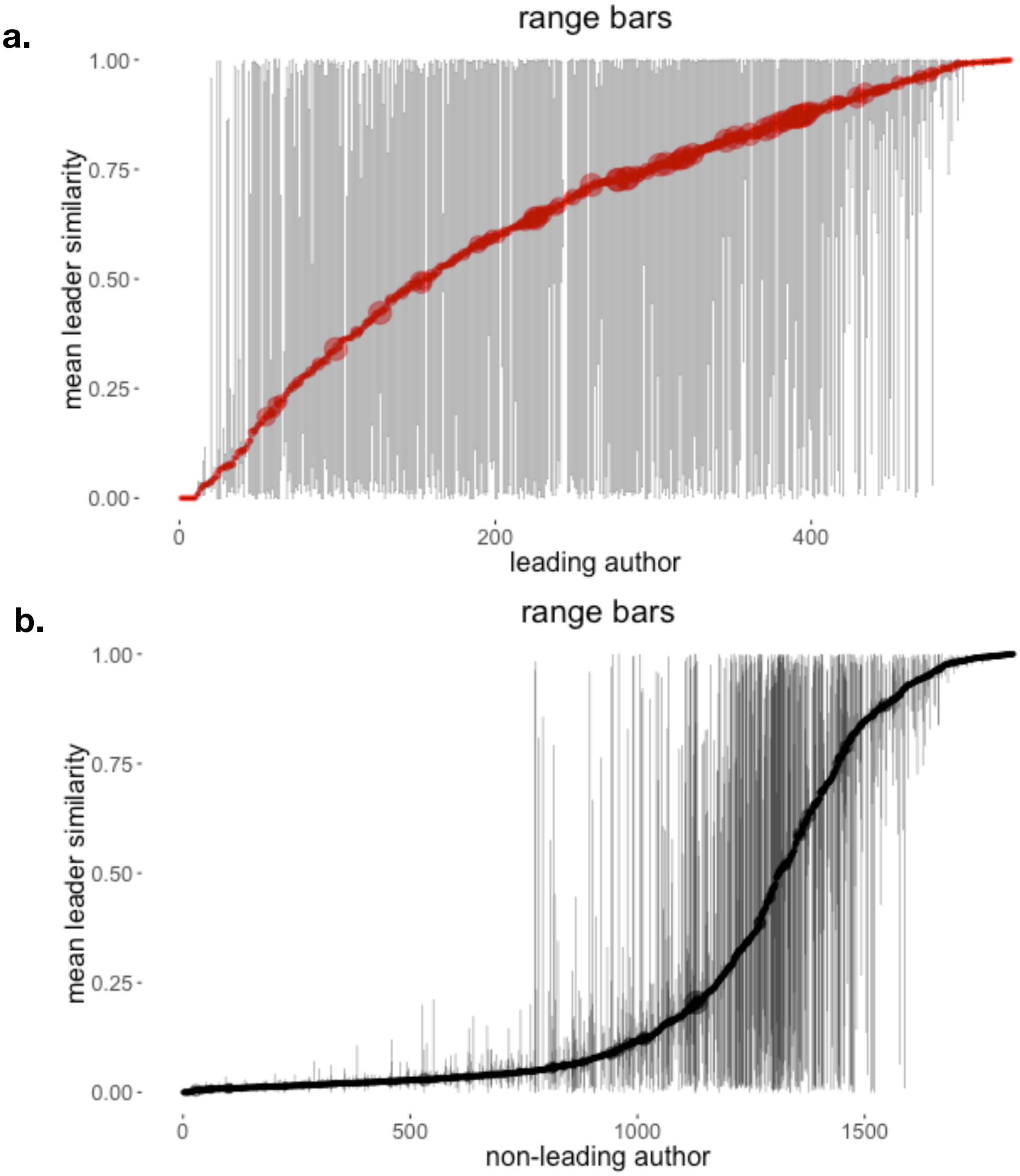


Figure 4.9 – (a) average values and range bars for the distribution of similarities to current leader for leading authors and (b) non-leading authors

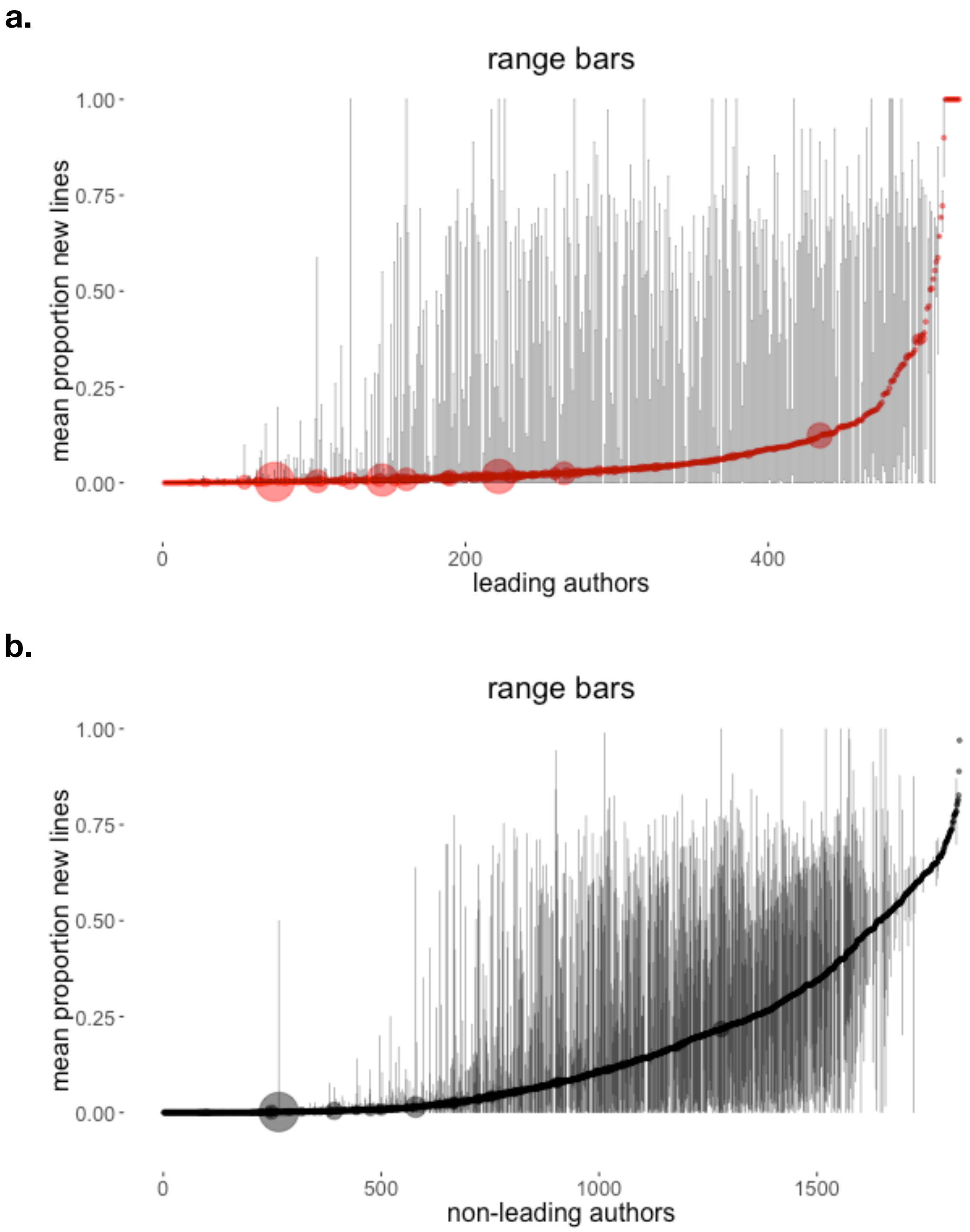


Figure 4.10 – (a) average values and range bars for the distribution of the proportion of new lines for leading authors and (b) non-leading authors

This indeed becomes evident when comparing the use of novelty between leading and non-leading authors (Fig. 4.11). Leading authors displayed a higher average similarity to the current leader than non-leading authors (Wilcoxon W(2353)= 382380, p<0.001), and they introduced a smaller proportion of novel lines on average, compared to the non-leading authors

(Wilcoxon W(2353) = 720250, p<0.001). This mirrors the results presented in Figure 4.5, indicating that better performing individuals introduced less novelty on average.

Nonetheless, leading authors showed a much larger variation of solutions than non-leading authors (Fig 4.11b). Leading authors displayed a higher range of similarity to the current leader authors than non-leading authors (Wilcoxon W(2353)= 818580, p<0.001), and a higher range of novel lines (Wilcoxon W(2353)= 671260, p<0.001), suggesting that the solutions introduced by leading authors were in fact more variable than the solutions of the less successful authors. So although, on average, leading authors tend to use introduce less novelty, they explore the solution space more broadly.

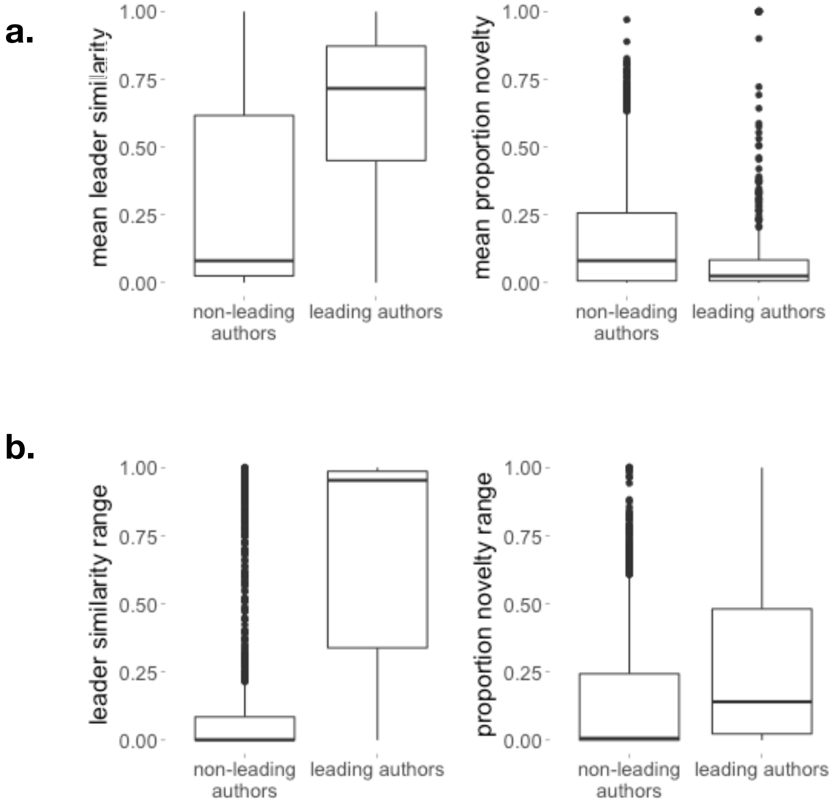


Figure 4.11 – (a) distributions of average leader similarity and average proportion of novelty for all non-leading and leading authors; (b) distributions of leader similarity ranges and proportion of novelty ranges for non-leading and leading authors

4.3.2. Influence

The influence measure accurately captured the patterns of similarity over time observed in Chapter 3, and was strongly correlated with the similarity to the current leader (Pearson R = 0.8, p < 0.001, Fig. 4.12).

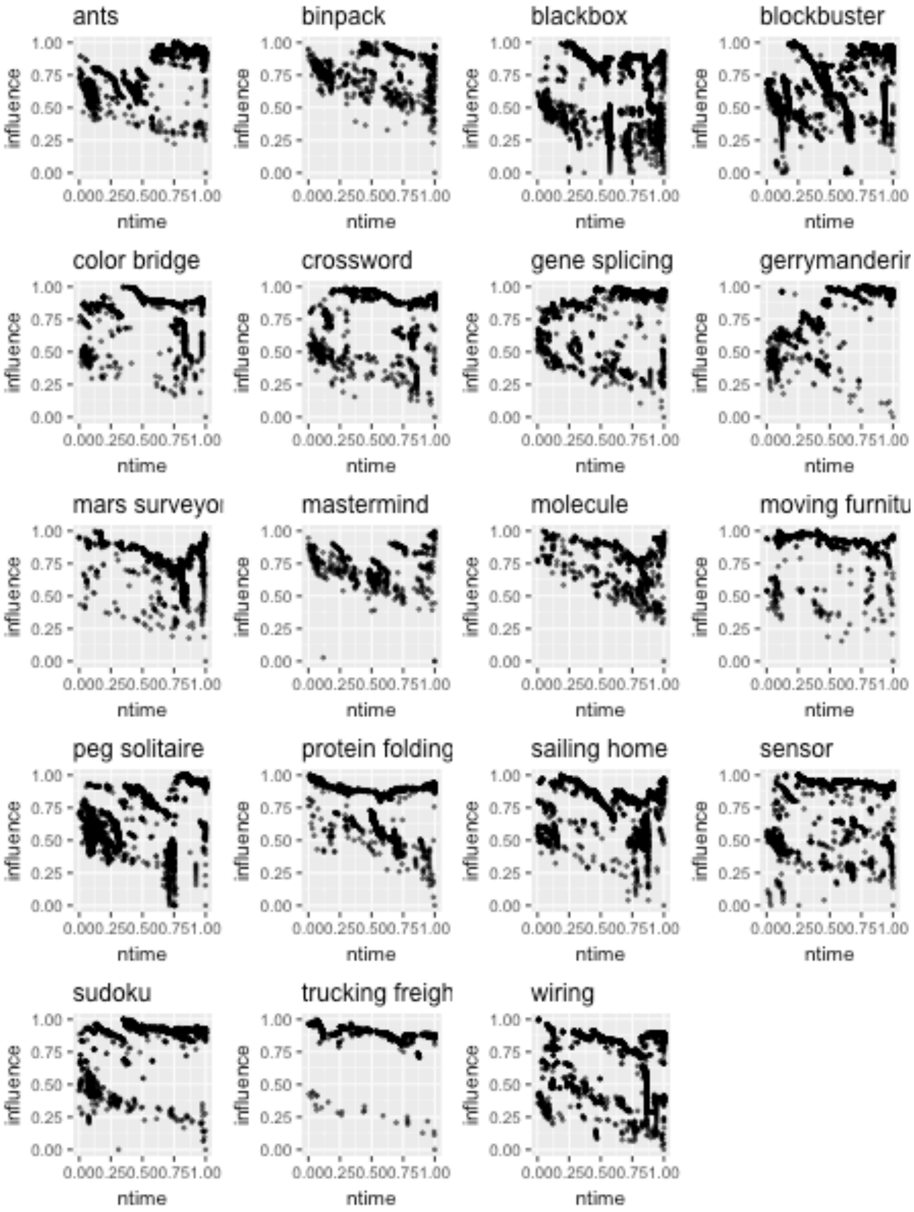


Figure 4.12 – influence (log-transformed average similarity between each entry and all the subsequent entries) for all passed entries submitted from day 3 onwards in all 19 contests

The between and within-individual variation in influence mirrors the patterns of similarity observed in the previous section – it seems that leaders and more active authors display higher variation in the influence of their entries, a sign of more exploratory behaviour (Fig. 4.13).

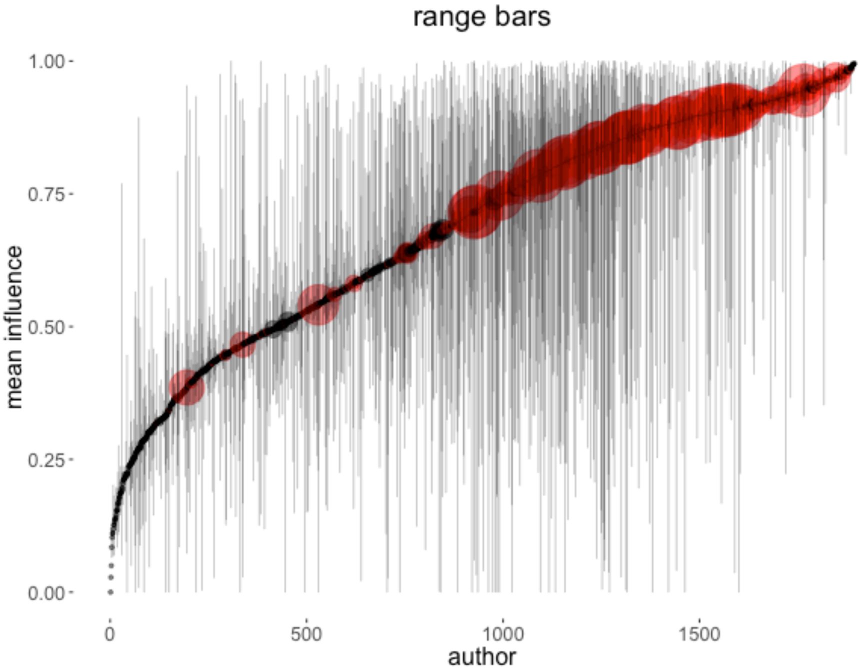


Figure 4.13 – average values for the distribution of influence for all authors in all contests, and bars spanning the range of each distribution. The size of the points is proportional to the number of entries submitted per contest, and the red points indicate leading authors.

Influence was associated with performance both at the entry level and individual level (Fig. 4.14). As expected, leading authors on average had a significantly higher influence than non-leading authors (Wilcoxon W = 195280, $p<0.001$) but this difference extends to entry-level influence – whether an entry was a leader affected the influence value of that entry. Results from the linear mixed model show that indeed leading entries had significantly higher influence than non-leading entries. Importantly, even non-leading entries submitted by leading authors had significantly higher influence than entries submitted by non-leading authors (Table 4.2), even when we control for score difference. The increase to an entry's influence due to its submitter being a leading author was slightly smaller than the increase associated with the entry being a leading entry – becoming a leading entry essentially doubles the influence of an entry compared to the entry merely being submitted by a leading author without managing to take the lead. Nonetheless, the increase associated merely with a leading author is detectable and significant. Therefore, leading authors submitted entries that had a higher effect on other participants, even when those entries were not the best available to copy and even when variation in actual score was accounted for. This indicates that a prestige-type effect is taking place in the contests, with authors who manage to take the lead at least once forming reputations that influence how the other individuals copy them.

Fixed effects	Estimate	Std. Error	t-value	p-value
(Intercept) Non-leading author Non-leading entry	**0.68**	**0.014**	**46.9**	**<0.001*****
Leading author Non-leading entry	**0.13**	**0.009**	**14.05**	**<0.001*****
Leading author Leading entry	**0.16**	**0.009**	**16.48**	**<0.001*****
Score increment	**0.24**	**0.006**	**41.74**	**<0.001*****

Table 4.2 – results for fixed effects from linear mixed model influence ~leader_group + increment + (1|contest:author)

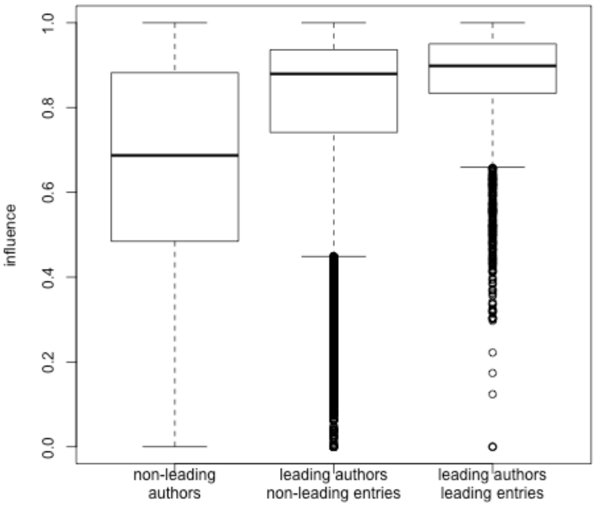


Figure 4.14 – entry-level influence distribution for entries submitted by non-leading authors, non-leading entries submitted by leading authors, and leading entries submitted by leading authors

4.3.2.1. Cross-contest reputation

Out of the total of 1416 unique authors, more than 83% only participated in one contest. The numbers of participants sharply decrease as the number of repeated contests increases, but there were still individuals who took part in 8 or 9 contests, with one participant competing in 14 out of the 19 contests we are investigating (Fig. 4.15). In order to adequately capture within-participant variation and to ensure methodological validity, I chose to examine individuals who participated in more than 3 contests, which leaves us with a sample size of 51 authors.

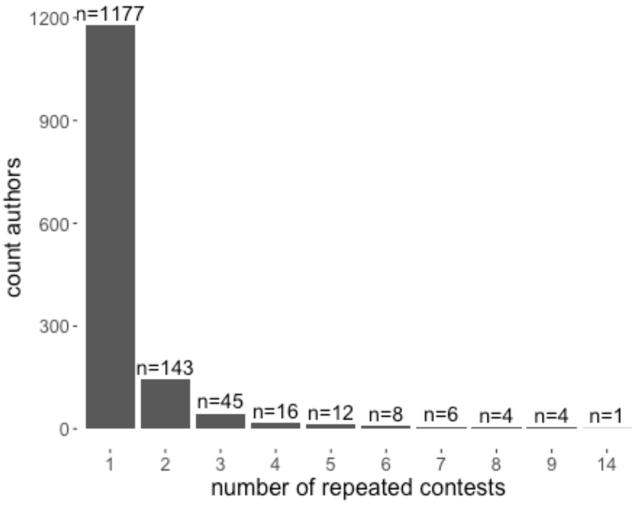


Figure 4.15 – number of authors who participated in 1, 2, 3, ... 14 contests

There was considerable variation both within and between all these repeat participants in terms of activity novelty, and performance (Fig. 4.16). Authors who participated in more contests, naturally, showed more variation in both the number of entries submitted and the number of entries that took the lead. For instance, some participants submitted on average 1 to 10 entries per contest, some usually contributed around 200 entries per contest, while the most active participant submitted between 400 and 1200 entries in the contests they competed in.

There was similarly large variation in the score increment relative to the current leader and, particularly, in the average leader similarity. Therefore different individuals seemed to show variation in their average strategy – for instance, a large number of individuals showed consistently high leader similarity in all contests (Fig. 4.16d). Yet they also showed different levels of variation across contests – some individuals were relatively consistent in their strategies, but there is no lack of examples of individuals who used widely varying strategies in different contests. Table 4.3 presents the results from the linear mixed-model testing whether the influence of an entry depends on the identity of the author who submitted and, importantly, whether this effect is present even for authors who have been leaders in a different contest from the one the entry was submitted in. That indeed seemed to be the case.

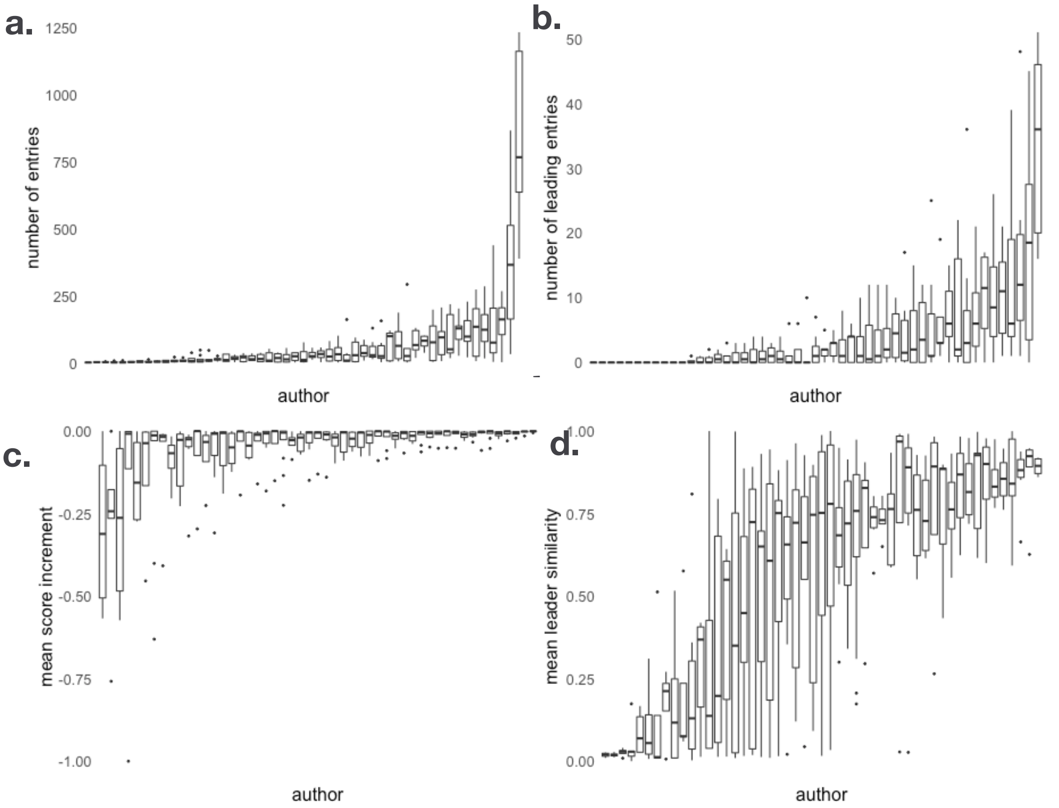


Figure 4.16 – (a) per author cross-contest distribution of the number of entries, (b) the number of leading entries, (c) per-contest average score increment relative to the current leader, and (d) per contest average similarity to the current leader. Each boxplot represents the distribution of the number of entries for (a) and (b), and average values for (c) and (d) for an author across all the contests the author participated in

Overall, leading entries had significantly higher influence than non-leading entries, and so did non-leading entries that have been submitted by an author who managed to take the lead in the same contest. Yet, although weaker, this effect held even for entries that did not take the lead, submitted by authors who did not become leaders in the same contest, but did at some point take the lead in a different contest. The increase in influence associated with the score increment was double any increase associated with the identity of the author or the leadership status of the entry, suggesting payoff bias was stronger than prestige bias. Entries that became leaders were associated with the highest increment, followed by entries non-leading entries that had been submitted by a leading author both within and across contests. The increment associated with a non-leading entry that had been submitted by a leading author in that contest was more than double than the increment of a non-leading entry submitted by a leader in a different contest, so overall the effect of leading in that contest is bigger than the effect of leading in a different contest (both for leading and non-leading entries). Nonetheless, leading in a different contest has a significant, albeit smaller effect on the influence of an entry. This suggests that cross-contest individual behaviour was significantly related to entry-level measures of influence, indicating that consistent individual characteristics affected how entries were copied, in line with prestige effects forming across contests through repeated participation.

Fixed effects	Estimate	Std. Error	t-value	p-value
(Intercept) Non-leading entry Non-leading author Not leading elsewhere	**0.675**	**0.014**	**45.35**	**<0.001****
Non-leading entry Non-leading author **Leading elsewhere**	**0.045**	**0.014**	**3.11**	**0.0019****
Non-leading entry **Leading author** Not leading elsewhere	**0.128**	**0.012**	**10.37**	**<0.001*****
Non-leading entry **Leading author** **Leading elsewhere**	**0.147**	**0.012**	**11.91**	**<0.001*****
Leading entry **Leading author** Not leading elsewhere	**0.156**	**0.013**	**11.92**	**<0.001*****
Leading entry **Leading author** **Leading elsewhere**	**0.176**	**0.012**	**13.77**	**<0.001*****
Score increment	**0.249**	**0.005**	**41.69**	**<0.001*****

Table 4.3 – results for fixed effects from linear mixed model
influence ~leader_group + increment + (1|contest:author)

4.3.3. Cross-contest improvement

The distribution of improvements within each contest, calculated as normalised score difference between the best entry and the baseline first entry in each contest, showed wide variability (Fig. 4.17), and ranged from a small percentage over the baseline provided (in contests like ‘Molecule’) to very large improvements of several orders of magnitude (for example in ‘Sudoku’ the score decreased from 25390 to 96.9).

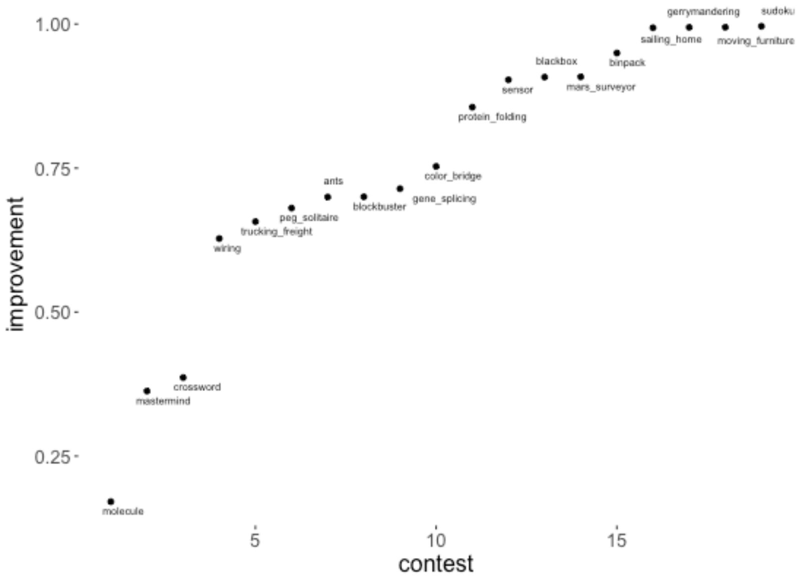


Figure 4.17 – score improvement relative to the baseline, for each contest

I tested the relationship between this measure of total contest improvement and both population size and our measures of the characteristics of individuals within each contest using non-parametric Spearman correlations. None of the relationships between improvement and the measures selected were significant. This is surprising particularly since there is an established relationship in the literature between cultural accumulation and group size, which would predict that contests with more authors and more entries will be associated with higher improvement, but that does not seem to be the case in this data. It is possible that improvement within a contest is a function of complex interactions between performance, activity, and novelty that the chosen measures failed to capture.

4.4. Discussion

This chapter has explored individual variation in the cumulative cultural setting of the MATLAB contests, how it relates to performance and copying, and how it affects contest improvement. There was considerable variation between individual participants regarding activity, performance, and the use of novelty in their solutions. More investment, in terms of time and how many entries an individual submits, was associated with better performance overall, but it was still possible for newcomers to join the contest and improve the overall score straightaway, suggesting that improvements in this setting were not dependent on experience.

The individual-level patterns of entry novelty did not indicate a clear split between individuals who prefer copying and individuals who prefer innovation, but rather described a continuous spectrum, in which individuals varied gradually in their proclivity to copy. This work is, then, another example of the importance of individual variation for the study of the evolution of social learning (Molleman, van den Berg and Weissing, 2014). Incorporating individual preferences for different learning strategies could lead to interesting interactions that models assuming homogenous behaviour might fail to capture. It could well be the case that different learning phenotypes are preferred in different environmental conditions (social learning is not necessarily an advantage in a highly variable environment, for example), so variation in learning strategies could arise from divergent selection under highly variable environmental conditions.

Results here suggest some individuals were consistently more successful than others, and that individuals who typically introduced more novelty were less successful overall. Individuals split into three broad groups with regards to how they commonly use novelty in their solutions: a group of extreme conservatives and a group of extreme mavericks, who rarely took the lead, and a third intermediate group of exploratory individuals who showed appreciable variation in their solutions, but who also regularly took the lead.

I have found that leading authors on average were more similar to the current leader and introduced less novelty, but they were also significantly more exploratory in their solutions, suggesting that diversity within individuals is positively associated with better performance. Reputation is a substantial reward in this contest setting – there is no cost to submitting a low performing entry, but introducing an entry that takes the lead is highly sought after, so it pays to experiment with solutions in order to find a well-performing one. Derex et al. (2013) discuss how this distinction between rewarding the highest score or the cumulative score affects exploratory behaviour. While rewarding the highest score (i.e. the highest single payoff) encourages exploring the fitness landscape, rewarding a cumulative score (i.e. the amount of payoff harvested during a given time) puts a considerably higher cost on sub-optimal solutions, which restricts exploration. A cumulative score is, arguably, more realistic as it reflects a trade-off between ensuring an accumulation of resources and improving technology to gain resources, for instance, but a high score reward would reflect how technological improvements can take place in an environment where failure is less costly. This raises interesting questions regarding whether different social structures could create different risk environments that would lead to between-group differences in behaviour.

I found that leaders had more influence on the patterns of solutions in the population, even through entries that did not take the lead. This effect extended across contests, such that individuals who had proved successful in other contests still managed to have higher influence even in contests in which they did not take the lead. While it is not clear if this phenomenon represents prestige per se, we can safely say there is some indicator of performance at the individual level, here signalled by the leader status, which can be picked up by the patterns of copying across time in each contest. By modelling the influence of leaders while controlling for the individual performance of each entry, I could establish whether leaders had higher influence merely as a result of submitting generally better entries, or whether leadership genuinely creates a reputational effect. The latter indeed seems to be the case, suggesting prestige-like effects in the copying of leaders. This is not a purely cross-domain phenomenon – the effect holds between contests, suggesting an individual's reputation builds in the MATLAB contest microcosm independently of the specific challenge, yet they all rely on the same programming expertise.

This analysis is vulnerable to the measure of influence we use. If it is the case that individuals progressively work on the same solution trying to improve it, then the non-leading solutions submitted by leaders will be similar to their leading solutions, and so will their subsequent similarity (which is what we used here to quantify influence). Therefore the non-leading entries submitted by leaders will have a higher influence not because they have a better performance, but because they are more similar to entries that do indeed have better performance and are therefore picked up by the population through payoff bias. This does not however change the fact that leading entries have a higher influence even when we control for entry performance and, importantly, does not explain why we find a leader effect across contests, suggesting that the leader status is indeed used to create a prestige-type effect.

Finally, I found no relationship across contests between population size, nor participant characteristics, and solution improvement, which is surprising given previous research discussed in the introduction. Indeed there is a great deal of debate around whether it is population size, group size, connectivity, or sociality that causally affect cumulative improvement in a given population (see Baldini, 2015 for an overview). In this case, the population is fully connected in theory, as all the entries are visible to all participants, but it is worth bearing in mind that the size of cultural repertoire in a contest quickly becomes too big for individuals to be able to inspect every entry, which is why they resort to copying the best entry. This could mean that the number of individuals used here is not a clear reflection of the 'group size' in the sense of the individuals or the cultural traits individuals interact with, but a superior alternative is not obvious. At the same time, the relatively small variability in terms of improvement between contests could be responsible for the fact that there was no relationship between improvement and variation in participant patterns. Although our dataset might not be specifically suited for answering this, the question whether individual variation promotes cumulative improvement is intriguing and merits further investigation.

Individual variation in behaviour is a topic that has only recently started to attract more attention in the field of cultural evolution. It has typically been neglected or treated as noise, and for good reason as it greatly complicates analyses and interpretation and introduces additional methodological difficulties. Nonetheless, the recent shift in the field towards acknowledging and attempting to explore individual variation as well as cultural variation is encouraging, as we expect individual variation to have important effects on the patterns of cultural evolution we witness. Mesoudi et al. (2016) suggest that assuming that social learning strategies are purely genetically specified could underestimate the speed of response to environmental variation, and support previous suggestions that the use of social learning can itself be culturally learned (Heyes, 2012a), which would speed up environmental adaptation, but could also contribute to faster spread of maladaptive traits. The importance of cultural differences has been recognised by behavioural scientists suggesting that a shift away from Western societies would question the universality of a great deal of current findings (Henrich, Heine and Norenzayan, 2010). The study of individual differences therefore has deep theoretical implications and will surely provide a fertile avenue for fruitful future research.

Chapter 5

An Experimental Investigation of Group Structure and Cumulative Culture

Abstract

Population size, connectedness, and sociality have been shown to be important factors shaping population-level dynamics of cumulative culture, but little work has attempted to address the mechanisms through which larger groups might promote an accumulation of more complex, more efficient culture. In this chapter I investigate experimentally whether group structure is such a mechanism that can lead to increased improvement in skill via an increase of cultural diversity, by modifying the MATLAB contest paradigm introduced in the previous chapters. I ran a similar programming competition with two conditions – a control that replicated previous contests, and an experimental condition, which involved splitting participants in three small groups for the first four days of the contest, and merging these groups for the last three days. Results show that the large group achieved better performance than the small groups overall, but through more incremental improvement, and increased activity levels. The large group showed more copying, but also more cultural diversity than the small groups, and our group structure manipulation did not increase diversity overall. Nevertheless, the diversity decreased in both conditions, through different processes – in the large group, diversity decreased as a result of convergence on similar solutions, while in the merged group condition the separate groups entertained different solution 'traditions', which were swapped for a new tradition once the groups were merged. I discuss the implications of group size on different cumulative cultural regimes.

5.1. Introduction

The previous chapters have shown that, in a cumulative setting, increasingly difficult improvements and a strong payoff bias drive populations to copy substantially, and to converge on increasingly similar solutions over time. This greatly reduces cultural diversity, as individual solutions are nearly indistinguishable. This is a paradoxical result, since human culture is evidently characterised by tremendous diversity and variability across groups. This chapter is concerned with experimentally exploring the potential causes of this paradox by focusing on how group structure affects cultural diversity and, consequently, incremental improvement.

The cultural evolution literature shows a great deal of effort dedicated to understanding whether population size promotes cultural accumulation, both through theoretical and empirical approaches. In 2004, Henrich developed a model to investigate the conditions under which skill in a cultural trait accumulates in a population, under the assumption that improvement in skill depends crucially on imitation errors (Henrich, 2004). In this model, all individuals could successfully identify and attempt to copy the person with the highest level of skill, z_t, but learning was not entirely accurate. Copying errors were modelled as a Gumbel distribution described by mode $\alpha - z_t$ and dispersion β, which means that, in a cumulative cultural scenario in which traits are generally very difficult to learn, most individuals will acquire a worse skill level than what they are trying to copy, but a small proportion of individuals will acquire a better one. Then, α represents the effect of low fidelity transmission, the systematic error that all individuals make when attempting to copy – a small α represents a skill that is easy to learn. On the other hand, β is the effect of inaccurate inference, and models the individual variation in learning accuracy.

Henrich concluded that the change in skill level depends, critically, on the population size. In this scenario, cultural evolution results in an accumulation of skill when the effect of transmission errors is overcome by the advantage of having a larger set of models, although this happens at different points for different types of skills. This means that under certain conditions, if the population size decreases enough, there are not enough individuals that manage to accurately copy and improve on the highest skill, curbing cultural accumulation. It could even be the case that, as the population size decreases, the erosion in knowledge is so high that the population loses artefacts and skills, as in the case of Tasmanian technology loss (Henrich, 2004).

Henrich's model is not without its critics (Henrich, 2006; Read, 2006), but has nonetheless been adopted and adapted to include population structure, migration, overlapping generations, and different social learning strategies (Powell, Shennan and Thomas, 2009; Bentley and O'Brien, 2011; Lehmann, Aoki and Feldman, 2011; Mesoudi, 2011c; Vaesen, 2012; Kobayashi, Ohtsuki and Wakano, 2016). These studies confirm the general finding that population size boosts cumulative culture. For example, Powell et al. (2009) adapt the Henrich model to investigate how group structure and connectedness affects the accumulation of beneficial culturally inherited skills. Using a simulated meta-population with sub-populations of different densities, connected through migration, the authors found that the accumulation of skills is not dependent on the meta-population size, but rather on the degree of interaction between sub-populations. Higher density leads to higher accumulation of skill and, importantly, higher migration rate does too. Migration has the same effect on cultural accumulation as increasing the size of an isolated population, as it increases the variation in skill level within a group, thus increasing the possibility that the group will improve over the mean skill level z. Even more, the authors show that model estimates of demographic changes fit archaeological data and explain the emergence of human modern behaviour in the Late Pleistocene.

This relationship between technological complexity and population size has been tested using data from real world populations too, with mixed results – some studies support a positive relationship between complexity and population size (Kline and Boyd, 2010; Collard, Ruttle, *et al.*, 2013), while others find no evidence (Collard, Kemery and Banks, 2005; Collard, Buchanan, *et al.*, 2013). For example, islands with small populations in Oceania are characterised by less complex fishing technologies (Kline and Boyd, 2010), but a study comparing several hypothesis regarding the driving forces promoting technological complexity finds that environmental risk, but not population size or residential mobility, predicts technological richness in recent western North-American hunter-gatherer populations (Collard, Buchanan, *et al.*, 2013).

The link between cultural accumulation and group size has been also investigated empirically (Caldwell and Millen, 2010; Derex *et al.*, 2013; Muthukrishna *et al.*, 2013; Kempe and Mesoudi, 2014), with the common conclusion that a larger group size promotes higher improvement or better preservation of skill, consistent with the modelling work. For example, Caldwell and Millen (2010) use the transmission chain paradigm to show that chains of participants exposed to three rather than one model improved an artefact more over time. Using a more complicated design, Derex et al. (2013) investigated experimentally the interaction between group size and task complexity. Groups of 2, 4, 8, or 16 individuals were seeded with two technologies: a simple task, which involved building an arrowhead whose efficiency was reliant on shape, and a complex opaque task, which involved building a fishing net characterized by complex interactions between several features. Each technology could be used to gain 'life units', which the participants aimed to accumulate. The participants could learn about artefact design by choosing to copy individuals from their own group. Results showed a qualitative difference between the small groups of 2 or 4 individuals, and the bigger groups. The simple task remained stable in the small groups, and improved in the larger groups, while the complex task deteriorated in the smaller groups, but remained stable in the larger groups. Even more, the authors showed that increasing group size maintained cultural diversity, as measured by the presence of both tasks in the group.

The main criticism of Henrich's model is that it does not incorporate population structure, but instead copiers possess full visibility and unhindered access to the best model. If, instead, we distinguish between population size and network size, and take into account how dense and connected the population is, it becomes clear that the rate of innovation and the spread of that innovation are two distinct factors that contribute separately to how a skill spreads and is maintained in a population, which are potentially mediated by different mechanisms. Baldini (2015) made exactly this distinction in a model that investigates the effect of population size on cumulative culture, but distinguished between population size (total number of individuals), network size (number of individuals accessible for copying), and connectedness (migration), finding that total population size has little effect on the accumulation of skill, but network size and connectedness do. This relationship was modulated by an interaction with the innovation rate – unsuprisingly, the importance of population size diminished at higher innovation rates.

Baldini's work (2015) raises interesting points regarding how the diffusion of information, and population structure, are key to the accumulation of culture. How rare innovations are and how they are transmitted are central issues, and this spread of behaviour is modulated by population structure. Cultural accumulation is therefore less affected by population size, and more by how the population is connected (Powell, Shennan and Thomas, 2009). Indeed this is starting to be confirmed empirically (Derex and Boyd, 2016), and it seems that social structure and the mode of the diffusion becomes crucially important once the assumption of one-shot learning is relaxed - if learners require more than one exposure to information in order to acquire it, for example, the social structure of the population is critical to the spread of that information, with more clustered networks ensuring more effective information spread (Centola, 2010).

Therefore much of the literature has been concerned with establishing whether larger groups promote an accumulation of more efficient culture, but to our knowledge the mechanisms that might support this link have yet to be investigated. Following Henrich's model, in which the population-level improvement in skill relies on the variation of skill between individuals, here I set out to investigate whether group structure might promote cultural accumulation via increased cultural diversity. Thus, if more diversity leads to an increased chance that the population invents a better solution, and group structure increases diversity, then manipulating group structure should lead to more improvement. I have shown that a large, fully connected group is characterized by cultural convergence, but if cultural diversity promotes cultural accumulation, then perhaps isolated groups would maintain more cultural diversity, which would in turn affect the patterns of cultural improvement at the population level.

To test this, I designed an experiment that follows a very similar structure to the previous MATLAB competitions (Chapters 3, 4), while manipulating group structure to test experimentally whether diversity affects performance in a cumulative cultural setting. The control condition replicated as much as possible the previous MATLAB contests, while the experimental condition consisted of three isolated small groups, which were merged halfway through the contest. This merge resulted in an overall total number of players comparable to the total number of players active in the large control group.

Firstly, this paradigm allows us to easily test whether group size affects performance in the programming contest by comparing performance within the small isolated groups with the large control group. Regarding cultural diversity, we expect that splitting participants into smaller groups should boost initial diversity across the whole population, since the presence of separate groups would mitigate the strong convergence effects witnessed in previous contests. If the population is structured, we might still see copying and convergence, but the separate groups would not necessarily converge on the same solutions. Thus, separate groups should maintain more diversity overall at the meta-population level. I tested this by comparing the patterns of similarity and novelty in different sized groups to establish whether there are differential levels of copying. I compared diversity patterns across the two conditions to confirm whether differential copying affected how the diversity changes. Once the groups were merged, I could compare the newly merged group with the control to test if the diversity patterns change when splitting and merging the small populations, and if these diversity patterns affect performance (i.e. improvement in the task). Therefore, this paradigm allows us to investigate group structure as a possible mechanism that could promote cultural diversity. This experiment tests two specific hypotheses: 1) larger groups are characterised by larger improvement and 2) group structure stimulates higher cultural diversity, which, in turn, leads to higher improvement. With respect to H1, I expect that larger groups will be characterised by larger improvement in the first 4 days before merging, but I remain agnostic regarding whether this difference in improvement is maintained after the entire 7 days. Rather, according to H2 I expect that the initial increase in diversity associated with splitting groups will boost performance so that, by the end of the 7 days, the improvement in the experimental condition will exceed the improvement in the large group condition.

5.2. Methods

5.2.1. Experimental procedure

I replicated the original MATLAB contests in an experimental setting with different group structure. Just like in the original contests, this used an NP-hard optimisation problem (see Appendix for details) and for the course of seven days, participants could submit solutions to the problem through an online interface, aiming to achieve the best score. The solutions were automatically scored upon submission using (similarly to Chapters 3 and 4):

$$score = k_1 * result + k_2 * e^{k_3 * runtime} \text{ (Equation 5.1)}$$

This is an optimisation problem, so *result* was the penalty calculated from the algorithmic solution that the solution aims to reduce, and *runtime* is the CPU time required for the algorithm to run. The *k* variables scaled and weighed the two values such that *result* contributed more to the score, while the *runtime* penalty ensured the entries would not take absurd amounts of time to be evaluated. The values used for the *k* variables were $k_1 = 1$; $k_2 = 0.1$; $k_3 = 0.05$. The score, as well as the full solution code, its name, the nickname of the participant, and the time of the submission were all public on the website.

I recruited participants through a mix of online advertisements, including specialised MATLAB newsgroups, and mailing lists. Before the beginning of the contest the participants were invited to make an account on the contest website and were informed of the general structure of the contest (i.e. duration, collaborative format, prizes), but only on the first day of the contest were they shown the actual challenge to be solved. At no point were they informed about the group manipulation – participants did not know they were split in groups. The winner in each condition (large control group and merged groups) was awarded the grand prize, which consisted of St Andrews University merchandise. In order to encourage activity throughout the contest, each day, in each group I awarded two prizes – a random entry and the best entry at a randomly picked time – each consisting of MATLAB t-shirts.

Prior to the beginning of the contest I randomly distributed all 132 of the signed-up participants into 4 groups, each belonging to one of two conditions. After the beginning of the contest, any new participants who joined were assigned randomly to a group. In all of the 4 groups, the participants could see all the above information (score, code, etc.) from all the other participants in their own group, but not the other groups. The first condition, the 'Large group' condition, consisted of initially 66 participants who could see each other's solutions from the beginning of the contest for the entirety of the week. The second condition, the 'Merged groups', consisted of 3 smaller groups of 22 participants who, for the first 4 days of the contest could only see the solutions of their own small group. From the 5th day on, the 3 small groups were merged, so that now participants from each small could also see the solutions of the other two small groups, but not the large group. A diagram of the experimental design is illustrated in Figure 5.1. This work was approved by the University Teaching and Research Ethics Committee of the University of St Andrews (approval code BL12543).

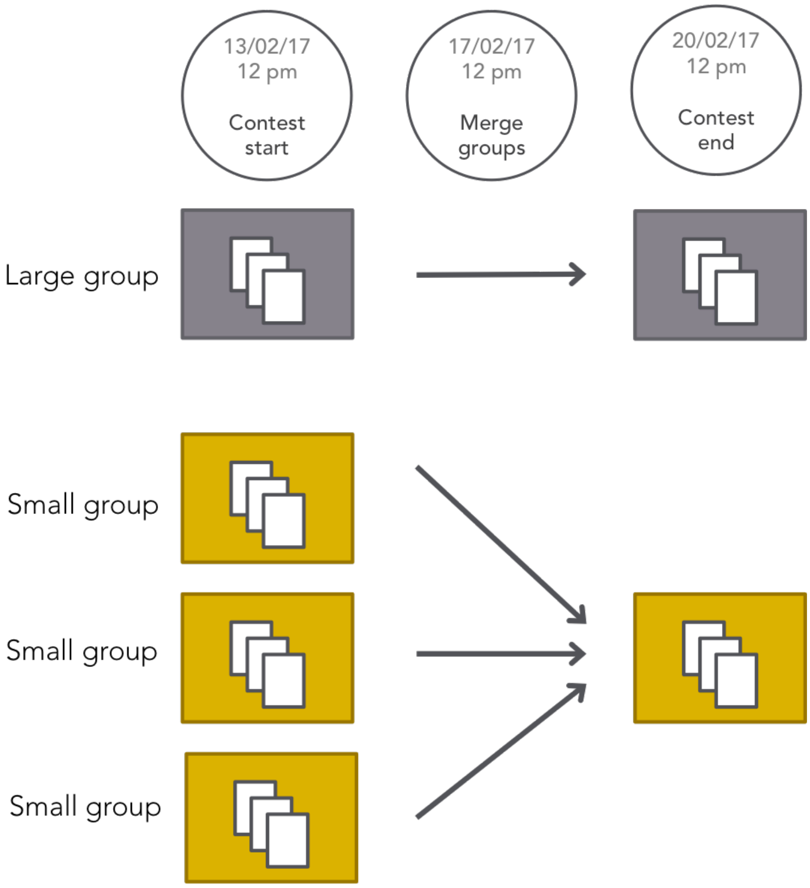


Figure 5.1 – experimental design

5.2.2. Analysis

For all the analysis I compared the large control group (henceforth ‘Group 1’), either before or after the merge date, with either the three small groups (‘Group 2’, ‘Group 3’, and ‘Group 4’), or the group formed by merging them during the experiment, in the experimental condition. It is worth noting that the composition of the control group was not manipulated before, or after the merge date.

5.2.2.1. Group size and performance

In order to test whether group size affects the degree to which the group improved its solutions over time, I compared performance across groups before merge (i.e. in the first four days of the contest). I used two measures of performance: total score improvement, to quantify the overall population-level improvement in solutions for the task given, and average individual performance, i.e. how well individual entries perform. This permits distinguishing between population-level performance and individual-level performance. For example, it could be that larger populations discover better solutions overall, but individual solutions in the population typically do not perform as well as the population best.

In order to quantify absolute improvement, an initial baseline score value was needed to compare the other scores to and establish how much each group improved relative to. I used the first entry in each group as a baseline, relative to which the other scores either increase or decrease. In the large group, because the first entry’s score was an outlier, double in value compared to all other scores in all groups at the beginning of the contest, I instead used the score of the second entry as a baseline, which incidentally is equal to the score of the first entry in two of the small groups, and one point smaller than the score of the first entry in the third small group. No other groups showed such a large score difference between the first and second entries. I therefore used the same baseline value of 104044 for all four groups. A smaller score is an improvement relative to this baseline.

In order to quantify the performance of each individual entry, I calculated entry-level increments, similarly to Chapter 3 and 4, relative to the current leading entry, as the difference in score between the leading entry and the target entry – this results in a positive value for the entries that improve over the current leading entry's score, and a negative value for the entries that do not manage to improve the overall score.

Performance can also be measured by quantifying how many entries became leaders, i.e. improved the overall score at the time of their submission, and by quantifying the magnitude of those positive increments, which improved the score over the current leader. Thus it is possible to characterise how incremental the improvement in a group is. If, for example, two groups show the same decrease in score, but one is characterised by a larger number of leaders, this suggests a more incremental improvement, achieved through more steps, while a smaller number of leaders would mean the same overall improvement was achieved through fewer, larger steps. Separately, if two groups comprise the same number of leaders, but the leaders in one group are characterised by higher average improvements than the leaders in the other group, then naturally the overall improvement in the former group will be higher than the overall improvement in the latter.

5.2.2.2. Group structure and performance

In order to test whether the group manipulation implemented in the experiment did indeed affect improvement over time, I compared performance in the control group after the merge date (i.e. the last three days of the contest), with performance in the newly merged group, using the same measures of performance used in the previous section: (1) absolute improvement, calculated as the difference in score between the best entry in each group at the end of the contest and both the baseline (to quantify total improvement), and the best entry in each condition before the merge date (to quantify overall improvement in each condition after merge in the last 3 days of the contest); (2) individual-level score increment in both conditions after the merge data, to quantify typical individual performance; (3) number of leading entries, and the magnitude of the score improvements achieved by those entries, in both conditions, to quantify how incremental improvement was.

5.2.2.3. Similarity and novelty

In order to quantify the amount of copying in the two conditions, I used two measures of novelty. A relative measure of novelty in the context of the MATLAB solutions is the similarity between the entries – less similarity means more novelty. By inspecting the patterns of similarity over time in each group, I illustrated the patterns of convergence in solutions. I used the same variation of the Sørensen–Dice coefficient used in the previous to chapters in order to measure the similarity between two entries. The Czekanowski similarity (Bray and Curtis, 1957), is given by:

$$CZ_{ik} = 2\,\frac{\sum_{j=1}^{S} \min\,(x_{ij}, x_{kj})}{\sum_{j=1}^{S}(x_{ij}+x_{kj})}$$

(Equation 5.2)

where CZ_{ik} is the similarity between samples i and k, x_{ij} is the number of instances of species j in sample i, and x_{kj} is the number of instances of species j in sample k. For our analysis, each sample corresponds to an entry, and each species is a line of code.

A second measure of code novelty used here is the absolute number of lines of code newly introduced by each entry. I did this at group level, such that for the large group, a new line in an entry represented a line that had not been used by any other previous entries within the large group (i.e. it could have been used in the merged group, for example, but it would still be considered new in the large group). Similarly, a new line in the small groups before the merge date represents a line that had not been used in each of the small groups, respectively – therefore, we treat each of the three small groups independently. Finally, a new line in the merged group after the merge date represents a line that had not been previously used in any of the three small groups combined. Thus I measured novelty at the group level, but in practice there was vanishingly little difference between this approach and novelty at the condition-level, or even overall novelty in the entire contest, because there was very little overlap in solutions between groups. I normalised the number of new lines of code in each entry by the total number of lines submitted by each entry, to control for longer entries skewing the distribution. Therefore, the measure of novelty used is the proportion of lines of code each entry newly introduced in its respective group.

Finally, for each entry in each group, I recorded the similarity to the current leader at the time of its submission, or the previous leader in the case of entries that managed to take the lead. I used this measure to quantify how much tweaking behaviour takes place in each condition, as a higher proportion of high leader similarity indicates stronger payoff bias and more tweaking. This measure was also used to investigate the relationship between tweaking behaviour and performance at the entry level.

5.2.2.4. Cultural diversity

The experimental group manipulation allowed us to test whether group structure affects cultural diversity. I measured cultural diversity as the number of unique lines submitted in each group. If the solutions are more similar, a large number of lines should be reused as a result of copying, which would result in a smaller number of unique lines. If a group is characterised by a larger number of entries, and those entries are more complex, the group will naturally include a larger number of unique lines. To control for the fact that the large group might contain more, longer entries, I also present diversity as a proportion of the total number of unique lines introduced in each condition, i.e. the total number of unique lines introduced throughout the entire week in the large group, and the total number of unique lines introduced throughout the entire week in all three small groups, and the merged group. This experimental setup allowed me to ask several questions about the effect of group size and structure on cultural diversity.

Does group size affect diversity?

Firstly, a larger group could demonstrate more diversity than a small group. All things being equal, a larger group would be associated with more variation in terms of solutions, which should also increase diversity. I tested whether this was the case by comparing the large group and the small groups in the first four days of the contest, before the merge date.

Does splitting the population into groups increase diversity?

Secondly, dividing the population could generate more cultural diversity as separate groups potentially settle on different traditions. I tested this here by comparing the diversity in the large group with the overall diversity in the three small groups pooled together, before the merge date. This provided evidence about whether the small groups entertained different solutions or whether small groups naturally introduced the same, perhaps simpler, solutions.

Does diversity decrease after merge?

Thirdly, after merging, I expected the large group to display less diversity than the merged small groups. The reasoning is that while the large group converges on similar solutions, which decreases diversity, the merged group would still entertain a more diverse range of solutions, as players did have not as much time after the merging to evaluate and copy all the new solutions introduced by the merging event. This prediction was tested by comparing the diversity in the large group and the diversity in the merged group throughout the last three days of the contest, after the merge date.

How does diversity change over time?

Finally, I investigated whether the diversity in the large group overall changed differently over time compared to the diversity in the merge condition. It could be that even though diversity levels are comparable between conditions, the change in diversity over time is different, which is what this last analysis tests.

In the previous MATLAB contests, the cultural diversity decreased steadily over time. Here, I tested whether the differential group structure affected diversity change over time. Comparing the relationship between diversity and time in the large group and the three small groups speaks to whether group size affects the dynamics of cultural diversity. Similarly, comparing the small groups with the merged group characterises how diversity changes through splitting and merging events. Finally, comparing the large group with the merge group conditions overall (the three small groups pooled together and the merged group) indicates whether splitting individuals into groups actually generates more diversity than keeping the population homogenous.

Diversity over time per group

To investigate how diversity changed over time in finer detail in each group, I split the time period spanned by each group in ten equally spaced intervals. Therefore, each group was characterised by a total time duration represented by a numeric value ranging from 0 to the number of days the group was active for, and each of these durations was split in 10 intervals. For the large group, for example, the overall time duration ranged from 0 to 6.96 (i.e. almost 7 days of submissions), split every 0.69 time units (such that the first time interval ranged from 0 to 0.69, the second one ranged from 0.69 to 1.39, etc.). I rescaled each of these time intervals between 0 and 1 in order to be able to compare between groups, such that the actual values for the time intervals used for the statistical analysis were 0, 0.1, 0.2, etc. For each time interval in each group, I calculated the number of unique lines of code submitted in that interval, as a proportion of the total number of unique lines submitted in each group, respectively. This normalisation allowed us to compare diversity change across groups. I tested the relation between time and diversity using Spearman rank correlations.

Diversity over time per condition

Finally, I used the same analysis to compare diversity across conditions in order to establish whether dividing the population produces more or less diversity overall. I compared the diversity change in the large group condition with the diversity change in the merged condition, in which I pooled the data from the small groups. Therefore, the merged group data consisted of the code submitted throughout the whole contest, in the pooled small groups, and the merged group. Because splitting the data by condition resulted in more data overall, I split the time duration using the same protocol as before into 20 intervals. For each of the two conditions, and for each of the 20 intervals, diversity was calculated as the number of unique lines of code submitted in each interval, as a proportion of the total number of lines submitted in each condition. To establish whether the diversity changed differently in the two conditions, I ran two linear regression models with diversity as the dependent variable and time interval as the explanatory variable – one on the data from the large group condition, one for the data from the merged group condition.

5.3. Results

5.3.1. Activity

Although a balanced number of participants between the two conditions was attempted, participation was fully voluntary, and players could interact with the task as much as they wanted, or not at all. Throughout the contest, the real number of active players was much smaller than the prior number of signed up participants. In total, for the first four days before merging, the distribution of players per group was: 18 players in group 1 (the large group), 8 players in group 2 (small group), 3 players in group 3 (small group), and 5 players in group 4 (small group), submitting a total of 428 entries in the large group, and 113, 14, and 40 entries in the small groups, respectively. After the merge, 10 players stayed involved in the large group, and submitted an additional total of 462 entries, while 9 players contributed to the merged group a total of 90 extra entries (Fig. 5.2). Overall, the large groups consisted of 20 unique players throughout the entire week, while the small groups together before and after the merge consisted of 17 unique players.

There was a large difference between the two conditions in terms of activity, both regarding the number of entries submitted and the number of active players. The number of entries submitted in the large group was 4 times larger than the largest number of entries submitted in any of the smaller groups both before and after the merge, and some of small groups before the merge showed remarkably little activity (i.e. 14 entries in 4 days). Not unexpectedly, the larger group contributed more entries to the contest, but it seems like the relationship between group size and activity is not as simple as more players submitting more entries, since the difference in number of entries is disproportionate to the difference in the number of players. Even after the smaller groups had been merged, the number of entries contributed by this merged group was still proportionally smaller than expected from this number of players, compared to the larger group.

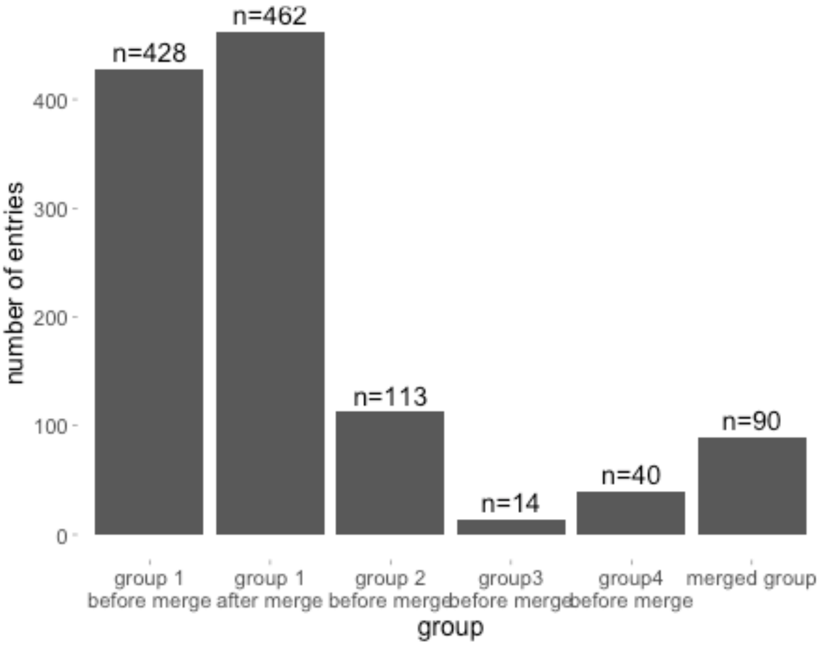


Figure 5.2 – number of total entries submitted in group 1 (large group) before and after the merge date, groups 2, 3, and 4 before merge (small groups), and merged group after merge

There was also a distinct difference in the patterns of activity per day between the two conditions (Fig. 5.3). The large group maintained a relatively stable activity pattern throughout the week, with a large spike in activity in the last day. The beginning of the contest displayed more failed entries, characteristic of initial exploratory behaviour until players settle on working solutions that they subsequently refine. In contrast, the three small groups showed much more variation. Group 2, which is also the largest of the three small groups, showed a relative increase in activity over the first 4 days, while groups 3 and 4 showed a drastic decrease.

The numbers reported above include both valid entries and entries that did not pass the evaluation because of algorithmic or runtime errors. Taking this factor into consideration, the differences in the activity levels become even more pronounced (Fig. 5.3). The smaller groups were characterised by a much larger proportion of failed entries, indicative of relatively smaller success compared to the large group. A potential explanation is that while the big group creates the same dynamic we have witnessed in previous contests, with entries resorting to copying the current leader and becoming increasingly successful and similar, the smaller groups do not manage to reach this stage, potentially for lack of activity.

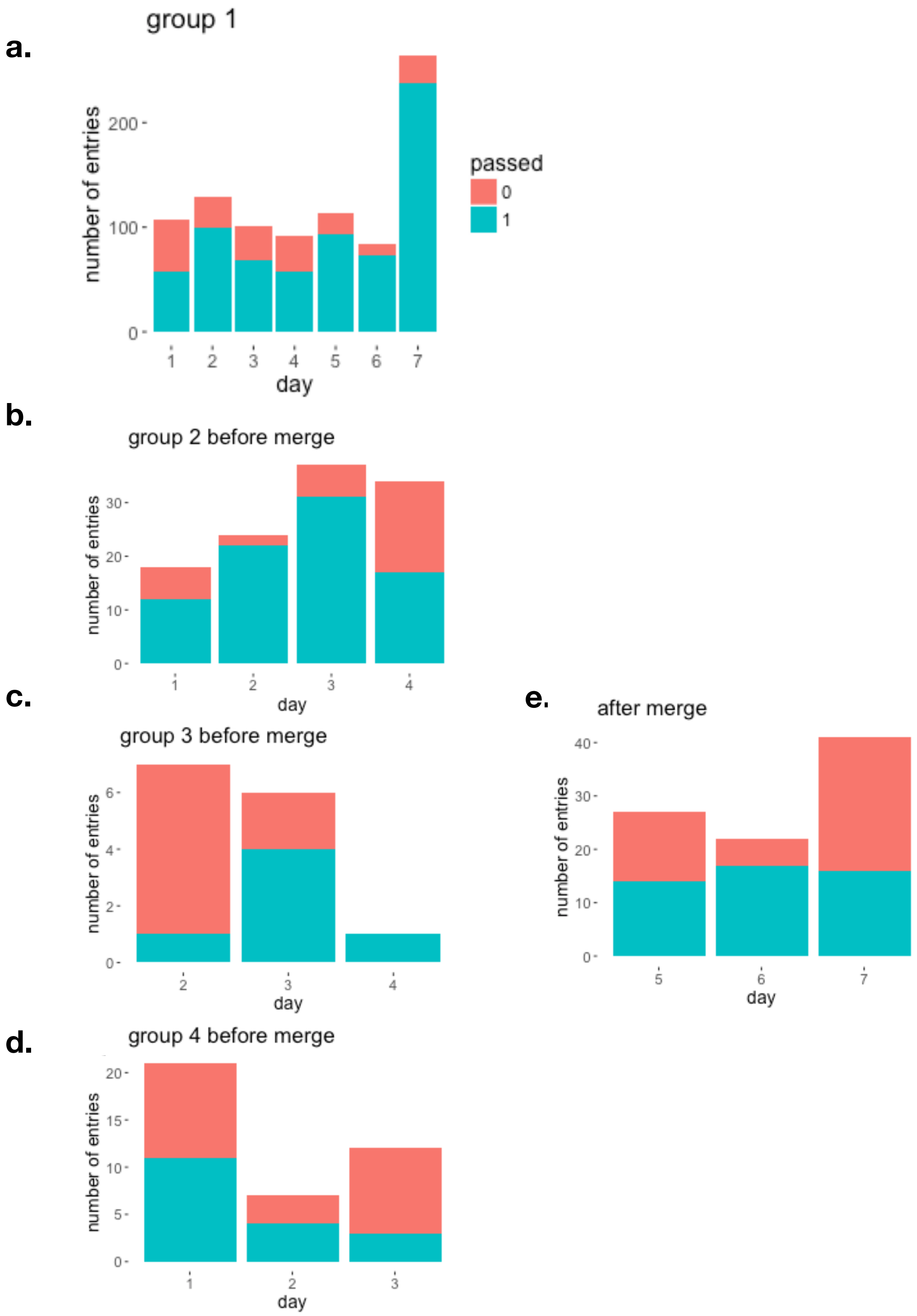


Figure 5.3 – (a) number of total entries submitted per day in group 1, (b-d) groups 2-4 before merge, and (e) the merged group. Passed entries in blue, failed entries in red

An interesting question is whether this increased activity in the larger group was due to the number of individuals or the identity of those individuals. The number of active players after the merge was similar for both conditions (Fig.

5.4, 5.5) – 10 in the large group, and 9 in the small group, but the larger group showed more variation in the first four days, with 18 different active participants submitting solutions. In the smaller groups, however, only 8, 3, and 5 participants took part before the merge, respectively. In the small groups 3 and 4, for example, there were even inactive days when no entry was submitted.

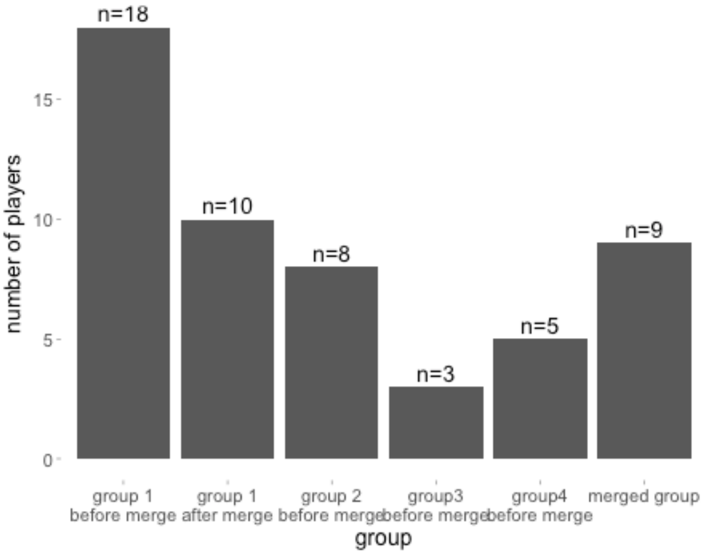


Figure 5.4 – number of total active players in group 1 (large group) before and after the merge date, and groups 2, 3, and 4 before the merge date, and the merged group

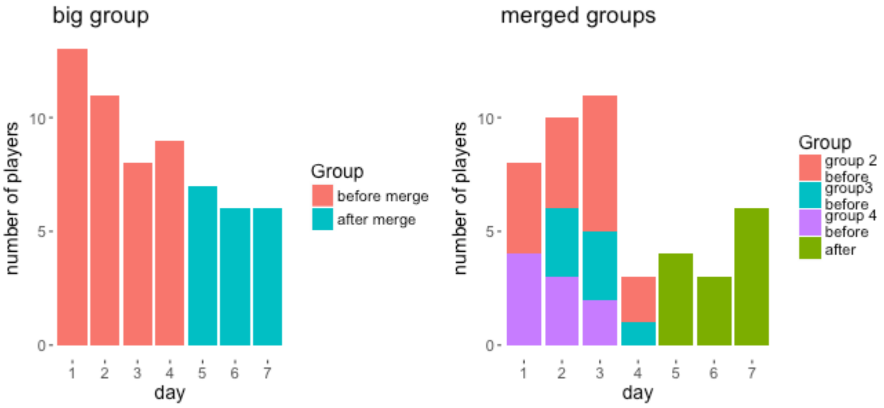


Figure 5.5 – number of active players per day in the big group (left) and the merged group (right)

Both the large group and the small groups saw a similar decline in the number of participants after the first four days – from 18 to 10 in the large group, and from 16 to 9 in the merged groups, but there did not seem to be a consistent pattern in the characteristics of the players who choose to leave the contest in the last 3 days of the contest. Both in the large group and the small groups, the players who quit varied from individuals who only submitted only one entry, to very active individuals. None of the groups was entirely abandoned – there were players from each of the small groups still competing in the merged group.

An explanation for the difference in activity between the two groups could be that, by chance, some of the players in Group 1 were more skilled, or more competitive, and drove this pattern in activity we witnessed. Indeed, in the last three days in both groups, the merged group showed an average of 10 entries per author, ranging between 1 and 27, with the three most active players submitting 21, 23, and 27 entries respectively in total in all three days. In contrast, in the large group participants submitted an average 40 entries each, ranging between 1 and 269. This distribution was skewed by two very active players in the large group, with a total of 146 and 269 entries respectively, submitted in the last three days. These two players also seemed to be among the best performing players in the contest –they scored in the top 3 average score per participant. This suggests it is not the number of participants, but the individual characteristics of the participants, that explain the differential patterns in activity levels.

5.3.2. Scores

5.3.2.1. Group size and performance – results before the merge

Scores improved in all groups over time. Figures 5.6 and 5.7 illustrate the log-transformed score over time throughout the entire contest, and the patterns of overall score decrease over time. These dynamics are very similar to the dynamics of score improvement witnessed in the previous MATLAB contests presented in Chapter 3. I tested whether there was a link between group size and overall performance by comparing scores in the large group and the three small groups before the merge date, i.e. throughout the first four days of the contest. After the first 4 days, the median score value across all groups was 86348.8, ranging between 77439 and 511847, therefore while there is considerable variation, on average entries improved approximately 17% relative to the baseline (i.e. the first entry, which scored 104044).

The best score in group 1 (the large group) was 77429, while the best scores in groups 2-4 were 82760, 89179, and 83186, respectively. This amounted to 25.58%, 20.46%, 14.29%, and 20.04% improvement relative to the baseline, respectively. Therefore, after the first four days, the large group improved more than any of the small groups, as predicted. Due to the small sample size of N=4 I did not attempt to test whether difference in improvement is statistically significant, not statistically test whether group size predicts score. Nonetheless, the patterns of improvement in the large group are convincingly different from the patterns in the small groups, but future work should attempt to formally disentangle these questions through larger sample sizes.

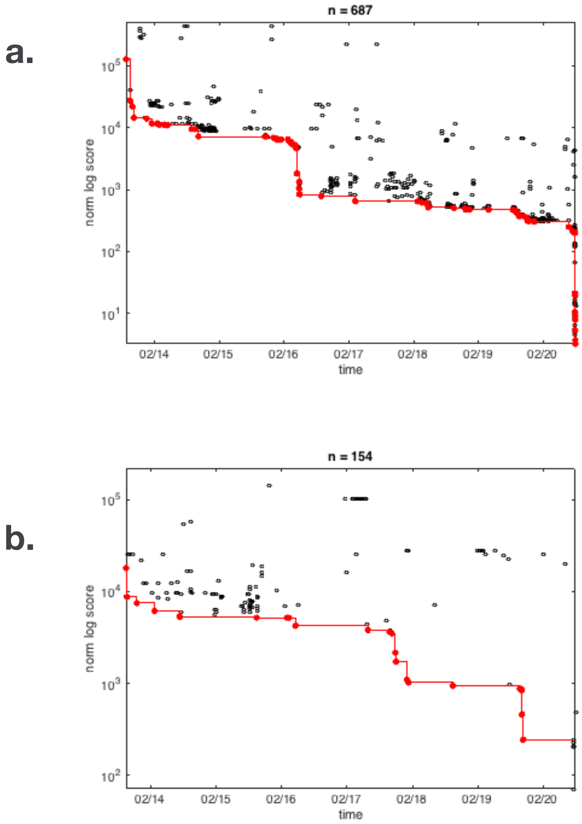


Figure 5.6 – (a) log-transformed scores over time in the large group condition and (b) the merged group condition throughout the whole contest. The merged group condition plot pools the data from the 3 small groups for the first four days. The red line follows the leading entries (i.e. entries that improve the overall score)

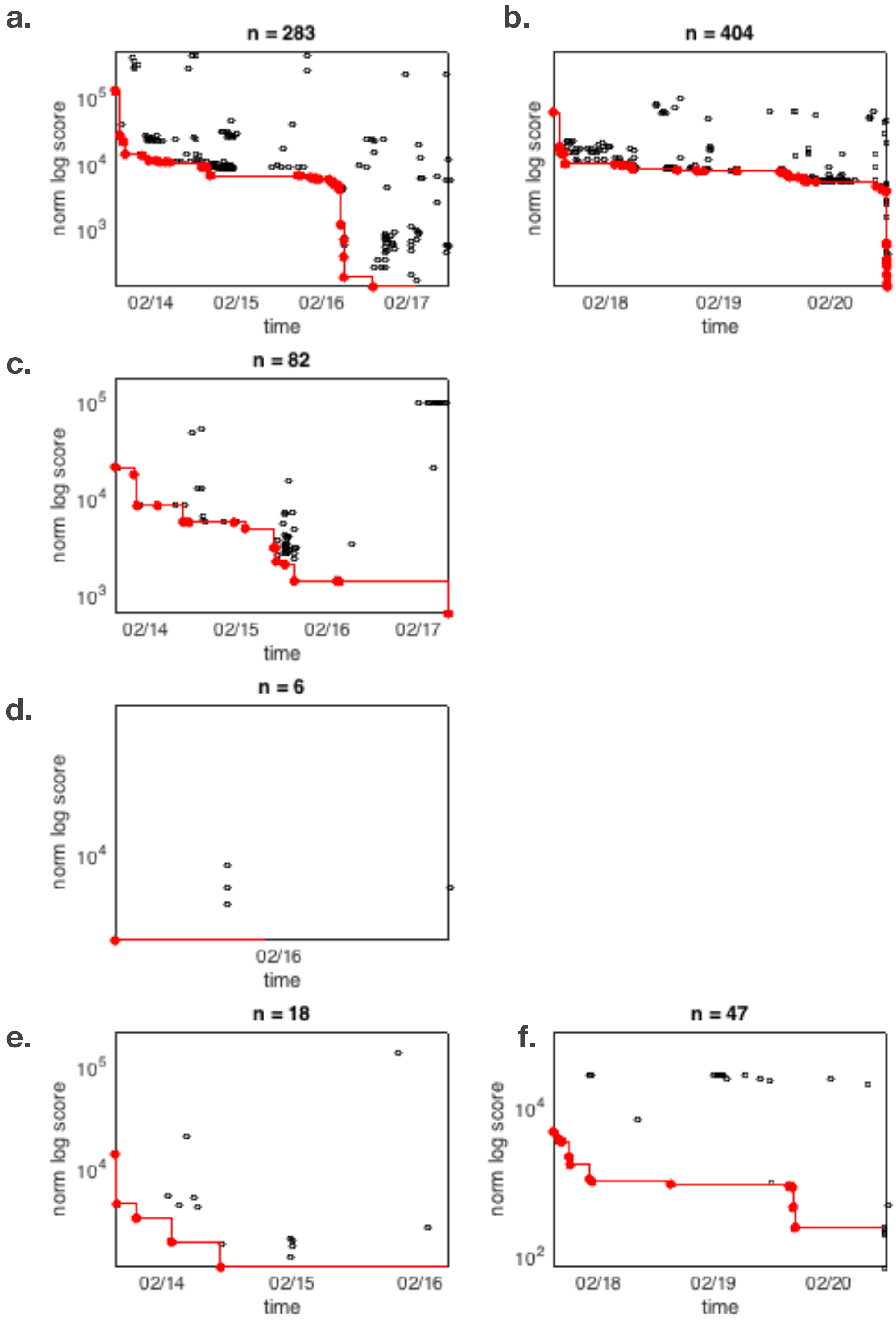


Figure 5.7 – (a) log-transformed scores over time in the large group before and (b) after the merge, and (c-e) in the small groups 2-4 before merge and (f) after the merge. The red line follows the leaders in each respective group

5.3.2.2. Group size and individual performance

Moving on to discuss individual-level performance, Figure 5.8a illustrates the score distributions in the four groups before the merge date, and Table 5.1 presents mean and median values for the scores in all four groups, as well average and median percentage improvements relative to the baseline. Median scores were very similar for group 1, 2, and 4. Group 3 performed more poorly, but there was little difference in the other three groups, suggesting individuals on average perform comparably between conditions. For instance, group 1, the large group, and group 4 manage a similar median improvement.

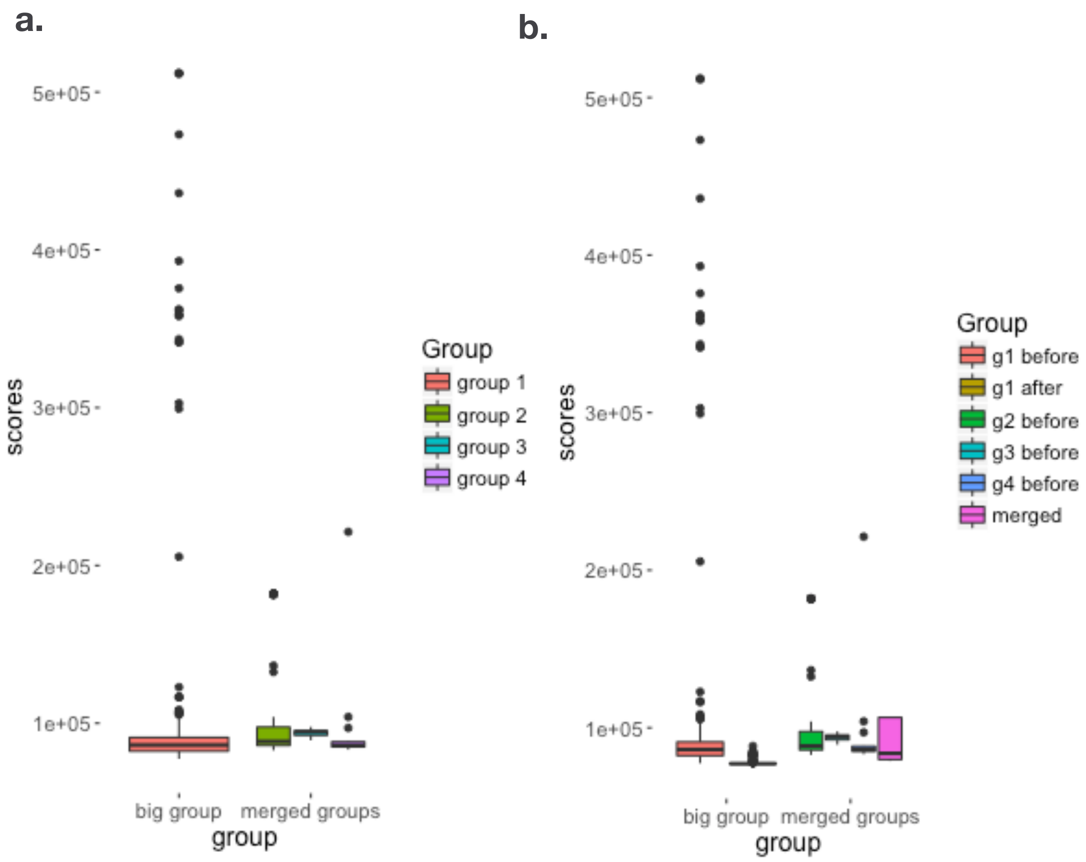


Figure 5.8 – (a) score distributions for the four groups (group 1 – large group, groups 2-4 – small groups) before the merge, and (b) before and after the merge

This suggests that although the large group managed to find a better absolute solution, there was no impact of group size on the typical individual performance of the entries in each group. When considering the average score, individuals in the large group actually performed the worst, with an average score that represented a decline in performance relative to the baseline (Table 5.1). This was caused by the fact that the large group exhibited considerable variation in performance across entries, as the score distribution also illustrates (Fig. 5.8a). The scores in the large group varied widely, as the largest score is almost 7 times larger than the smallest score; on the contrary, the difference between the largest and the smallest score in Group 3, for example, was a mere 9%.

Group	Mean	Mean improvement	Median	Median improvement	Standard deviation
Group 1	**105967**	**-1.85 %**	**86187.66**	**17.16 %**	**74839**
Group 2	**105624.7**	**-1.52 %**	**88468.93**	**14.97 %**	**35796**
Group 3	**93855.46**	**9.79 %**	**94508.16**	**9.16 %**	**2991**
Group 4	**95105.36**	**8.59 %**	**86133.96**	**17.21 %**	**31897**

Table 5.1 – mean and median scores, and mean and median improvements relative to the baseline in the 4 groups, before merging

With regards to the number of leading entries per group, the large group was characterised by a much larger absolute number of leaders, 49, compared to 18 leaders in Group 2, 1 in Group 3, and 5 in Group 4. However, when normalising these values by the number of passed entries submitted in each group, only 17% of the entries in Group 1 manage did take the lead, compared to 22%, 17%, and 28% in the other three groups (Table 5.2). Therefore, when controlling for the overall activity levels in terms of entries submitted, the large group was again not performing better on a per capita basis, potentially because of the stronger competitive environment.

It could be the case that the number of improvements in the large group was not proportionately larger, but the magnitude of those improvements was, leading to higher improvement overall. To address this I isolated only the entries that improved on the current leading score (Table 5.2). The mean and median values for improvements across groups did not support the hypothesis that the larger group was characterised by bigger improvements on average. In fact, the average improvement value in the large group was comparable to the other groups, but the median value was much smaller. This indicates that, opposite to our expectation, the large group was actually characterised by more improvements, but smaller in magnitude, compared to the small groups.

To summarise, the larger group achieved better performance overall at the end of the first four days through more, smaller improvements, but the individuals entries submitted in the larger group were not better, in terms of score improvement, than the entries in the other groups on average.

Group	Number of improvements	Proportion improvement	Mean improvement	Median improvement	Standard deviation
Group 1	**49**	**17%**	**2613.4**	**80.9**	**14479**
Group 2	**18**	**22%**	**1182.4**	**388.33**	**2274**
Group 3	**1**	**17%**	**2713.04**	**2713**	**NA**
Group 4	**5**	**28%**	**2770.8**	**1251.4**	**3680**

Table 5.2 – number of improvements, proportion of entries that improve out of the total number of passed entries, average and median improvement values in the 4 groups, before merging

5.3.2.3. Group structure and performance – results after the merge

If manipulating group structure had an effect on performance, this would translate into differential score patterns both at the population level and the individual level between the two groups in the last three days of the contest, after the merge date. There was much less variation in scores in the last three days of the contest, though scores decreased steadily (Fig 5.7b, 5.7f). In terms of overall absolute improvement, the large group still wins. The final best score at the end of the contest in the large group was 76776, which represented a 26.2% increase relative to the baseline, and a 0.8% increase relative to the best in the large group before merge. In the merged group, the final best score was 78952, which represented a 24.11% increase relative to the baseline, and 4.6% improvement relative to the best score in all small groups prior to merging (with value 82760). The large group was still performing better overall after the merge, but by a much smaller difference.

In order to explore individual-level performance, the score distributions for the two groups overall, and after the merge, are plotted in Fig. 5.9 (see Fig. 5.8b for a comparison with the distributions prior the merge). After the merge date, individuals on average performed much better in the large group than the merged group (Fig. 5.9a, Table 5.3). The mean and median scores in the large group were very small and very similar to the final best score in the entire contest. In the merged group, however, scores showed much more variation, and the average scores did not manage to improve relative to the best score in the group before merge. Therefore, contrary to the patterns witnessed before the merge date, here entries in the large group performed better on average.

Group	Mean	Mean improv. wrt baseline	Mean improv. wrt group best	Median	Median improv. wrt baseline	Median improv. wrt group best	Sd
Large group	**77546.2**	**25.47%**	**-0.15%**	**77183.22**	**25.82%**	**0.39%**	**1349**
Merged group	**92219.97**	**11.36%**	**-11.43%**	**83723.7**	**19.53%**	**-0.16%**	**12656**

Table 5.3 – mean and median scores, mean and median improvements relative to the baseline, and mean and median improvements relative to the best score before merge in each respective group, for the two groups, *after merging*

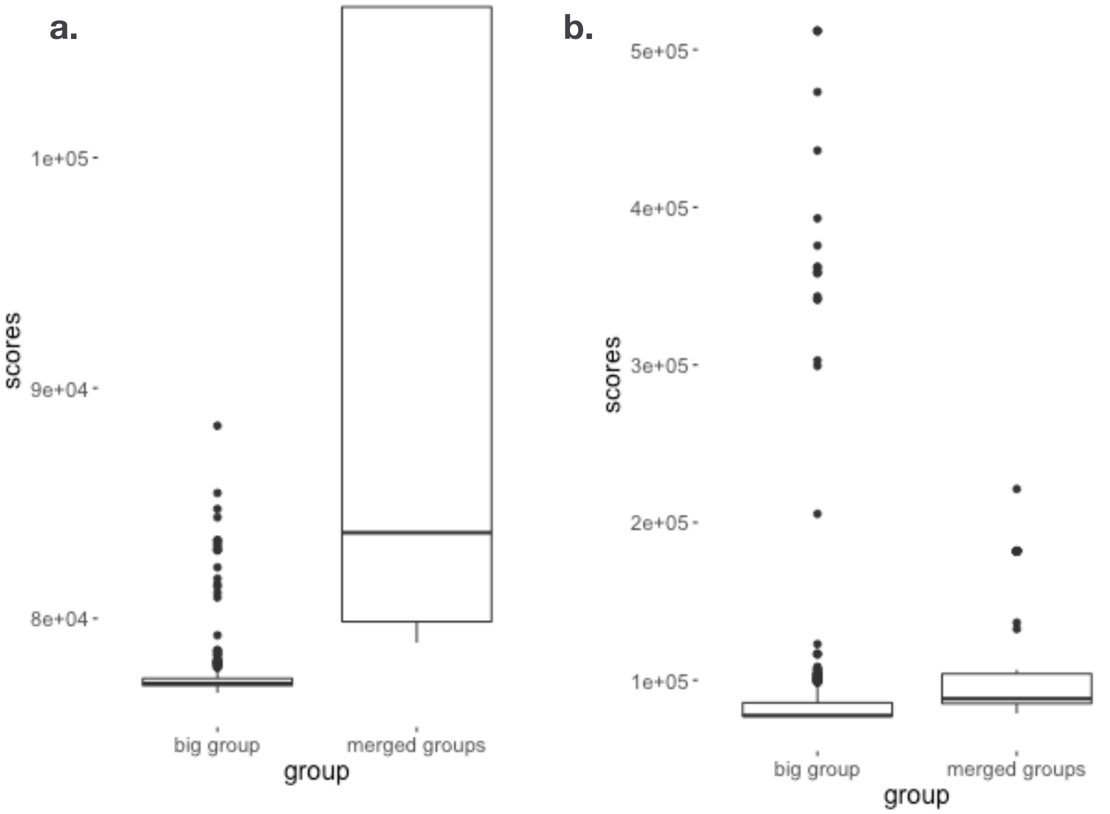


Figure 5.9 – (a) score distributions for the two conditions (big group and merged group) after the merge, and (b) over the whole contest (pooled data from the three small groups before merge, and the merged group after)

With respect to how many entries became leaders in the two groups in the last three days of the contest, and how much those leading entries improved the score on average relative to the current leader, the pattern found before the merge date held after the merge date as well (Table 5.4). The large group was characterised by a very large number of improving entries that only represented 11% of all passed entries, while the merged group only improved through 14 entries, almost 30% of all passed entries in this group. The median improvement value in leading entries in the large group was 5, while the median improvement in leading entries in the merged group was 202. These two results further reinforce the picture that the large group introduced many, but relatively small improvements compared to the merged group. Note that all these mean and median improvements are very much smaller compared to the pre-merge improvements presented in Table 5.2, indicative of the fact that improving is generally more difficult in this later part of the contest.

It is worth noting that the number of entries submitted post-merge date in the large group condition was almost 10 times larger than the number of entries submitted in the same period in the merged group condition, which suggests that the high activity levels observed pre-merge in the large group were maintained, while the merged group does not see this much activity, even if the groups were nominally similar in size.

Group	Number of improvs.	Proportion improvs.	Number of entries	Mean improve.	Median improve.	Standard deviation
Large group	**46**	**11.4%**	**404**	**14.18**	**5.07**	**28.5**
Merged group	**14**	**29.8%**	**47**	**340.8**	**202**	**389.9**

Table 5.4 – number of improvements, proportion of entries that improve out of the total number of passed entries, average and median improvement values in the 2 groups, *after merging*

5.3.3. Similarity and novelty

The big group was plainly characterised by many, small improvements, and a large number of entries lying very close to the leader line (Fig. 5.7), which suggests considerable copying. Group 2 somewhat showed this dynamic, but the patterns broke completely in the other two small groups, and in the merged group – there was less convincing evidence of copying. The large group showed the tweak and leap dynamic so prevalent in the previous contests, while the small groups seemed to rely more on individual exploration and little social learning. This section addresses the patterns of novelty and copying in the two experimental conditions and how they relate to the patterns of improvement.

The differential patterns seen in the dynamics of score improvement over time between the two conditions are very clearly reflected in the patterns of code similarity across time in the two conditions. Figure 5.10 illustrates the Czekanowski similarity between all passed entries in the large group condition and Fig. 5.11 breaks these patterns up by group before and after merge. For ease of visualisation, I present here the relationships between passed entries only, but the patterns are very similar if we take all entries into account. The large group was characterised by a very clear dynamic of convergence on similar solutions over time. Entries converged on a solution initially, then switched to a more popular solution that stayed in the population throughout the whole contest.

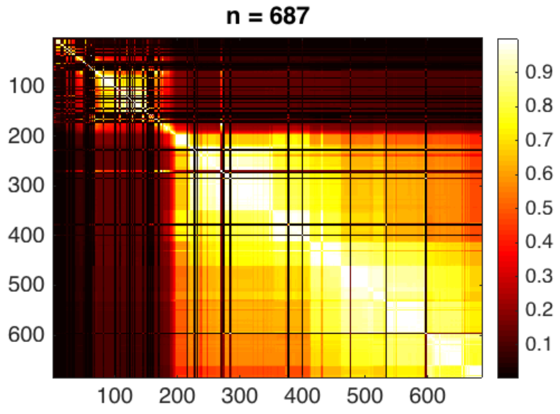


Figure 5.10 – similarity between all passed entries throughout the whole contest in the large group, ordered chronologically from left to right and top to bottom. Lighter colour indicates higher similarity

Indeed, in the last three days after the merge, the entries in the large groups showed overwhelmingly large similarity, clear evidence of copying (Fig. 11b).

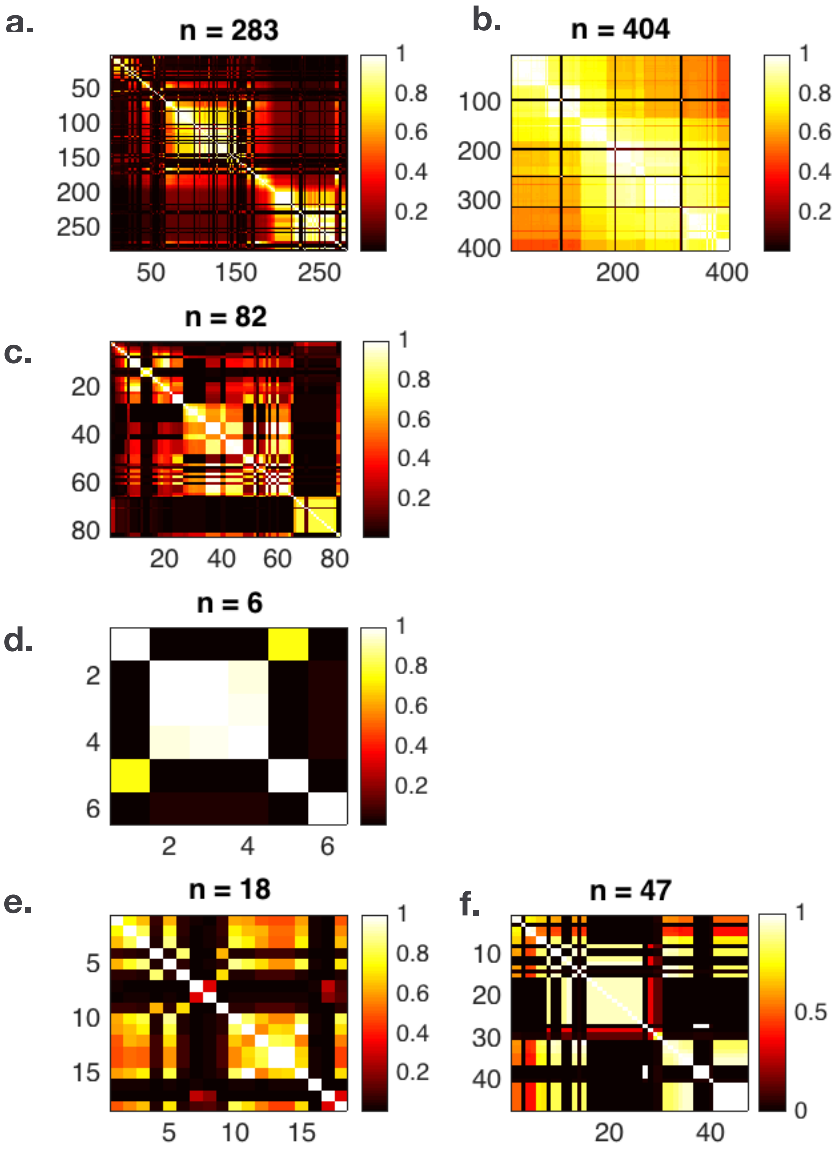


Figure 5.11 – (a) similarity between all passed entries throughout the whole contest, ordered chronologically from left to right and top to bottom, for the large group condition before and (b) after the merge, and (c-e) the three small groups before the merge, and (f) the merged groups

This pattern was still present, but not as strong and subject to more noise, in small Group 2 before merge (Fig. 5.11c), and to some extent in Group 4 (Fig. 5.11e, though the sample size was too small for a clear pattern to emerge). After the merging date, the merged group showed signs of convergence for small period of time, but this convergence was less convincing because of the small number of entries (Fig. 5.11f). In our dataset, the larger groups showed stronger signs of convergence than the smaller groups. The difference between the large group and the small groups before and after the merge is, at least, clear evidence that the processes at work in the large group, perhaps a matter of group size, motivation, or an interaction between the two, are related to strong convergence in the population.

The difference in the entries' reliance on copying suggested by these similarity matrices is further confirmed by the distribution of novelty per group (Fig. 5.12). The large group condition was characterised by significantly less novelty as measured by the proportion of novel lines than the merged group condition, both before the merge date (Wilcoxon $W = 8922$, $p<0.001$), and after the merge date (Wilcoxon $W = 2068$, $p < 0.001$). Entries in the large group introduced generally little novelty in the first half of the contest, with relatively large variation between entries. The median value for the proportion of novelty in this group was very small, 0.56%, ranging between 0 and 80%. This variation was purely due to initial high novelty in the group, prior to the population settling on a successful solution. After the merge date, the proportion of novel lines in the large group entries was minuscule, with a median value of 0.073% (though bear in mind that the merge date did not change visibility in the large group – this is result is purely due to convergence).

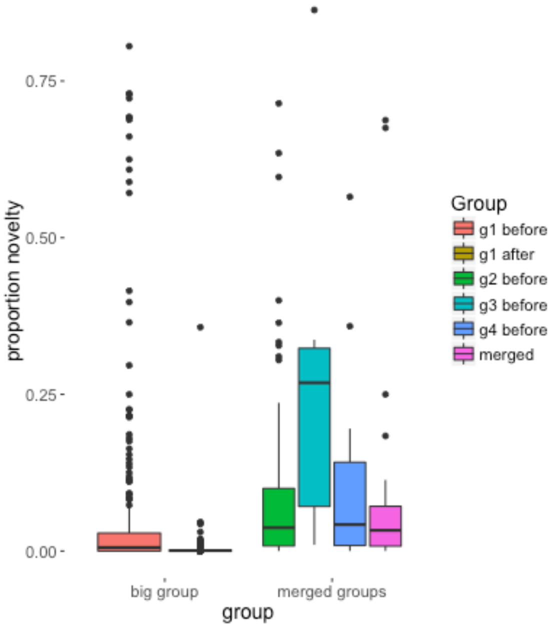


Figure 5.12 – Proportion of novelty for the large group before and after the merge date (left), and the three small groups before the merge, and the merged group (right)

The proportion of novelty was visibly much larger in the merge condition, both before and after the merge. The typical proportion of novelty remained higher in the small groups, because there was less drastic convergence and there were generally fewer entries to be copied. The median values in Groups 2, 3, and 4 were 3.8%, 28.7%, and 4.22%, respectively. After the merge, the median proportion of novelty in the merged group was 3.3%, still much larger than in the large group.

This difference in the proportion of novelty between the two conditions could be partly due to the fact that entries become much longer in the large group condition compared to the small groups. In the small groups before merge, the average length of an entry was 110 lines of code, while the average length of an entry in the large group before merge was 405 lines of code. After the merge, entries in the merged group were 135 lines long on average, but entries in the large group were 1261 lines long on average. This difference in length is, again, due to the extensive amount of copying taking place in the large group, but not in the small groups. As entries are being copied and added to, they become increasingly longer. This phenomenon does not take place in the small and merged groups, as the tweaking behaviour does not have a chance to get established and develop.

One final piece of evidence for differential convergence patterns comes from the differences between groups concerning the similarity to the current leader. In previous contests we observed strong payoff bias as most entries copied the current leader and tweaked it. In this data, before the merge date, there was virtually no difference between the large group and the small groups in terms of entries' similarity to the current leader (Fig. 5.13; except for Group 3, the smallest group, which showed virtually no sign of copying the current leader). After the merge, though, the large group converged almost exclusively on copying the current leader, yet the merged group still showed considerable variation – most entries here did not copy the current leader. Therefore, the large group showed clear evidence of payoff bias and tweaking behaviour, as most entries submitted in the second part of the contest were extremely similar to the current leader, but the merged group did not show this pattern at all.

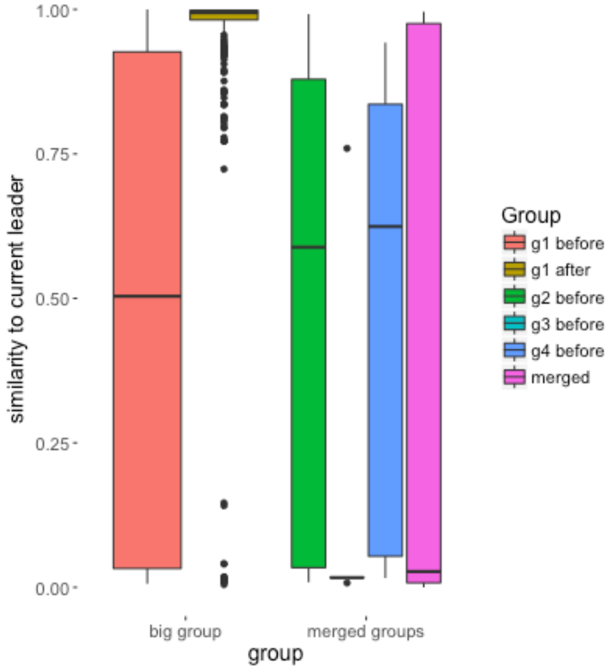


Figure 5.13 – Similarity to current leader for the large group before and after the merge date (left), and the three small groups before the merge, and the merged group (right)

There was a significant relationship between copying the current leader and performance. In all entries, there was a significant positive correlation between the similarity to the current leader and the score increment relative to the current leader (Spearman S = 44948000, $\rho = 0.53$, $p < 0.001$), indicative that payoff biased copying paid off - entries who copied the leader performed better. Overall, the large group condition replicated the results from the previous MATLAB contests (Chapter 3). After an initial period of code novelty, the population converged on highly similar solutions as a result of considerable copying of the current best entry. The evidence in the small groups and the merged group is much more variable. While some entries introduced little novelty and copied the current leader, this was far from being a majority trend. The small groups showed much more variation in terms of novelty, and less clear evidence of convergence over time. It is surprising that we did not observe convergence even after the groups have been merged (Fig 5.13), which was what we expected.

5.3.4. Cultural diversity

5.3.4.1. Does group size affect diversity?

The large group clearly entertained a larger repertoire of lines of code than any of the other groups (Fig 5.14a). Even after normalising within condition, the large group was still characterised by a much larger amount of diversity than the small groups (Fig. 5.14b). In fact, 82% of the number of unique lines of code in the large condition had been submitted in the first half of the contest. In contrast, the small groups each displayed much smaller diversity.

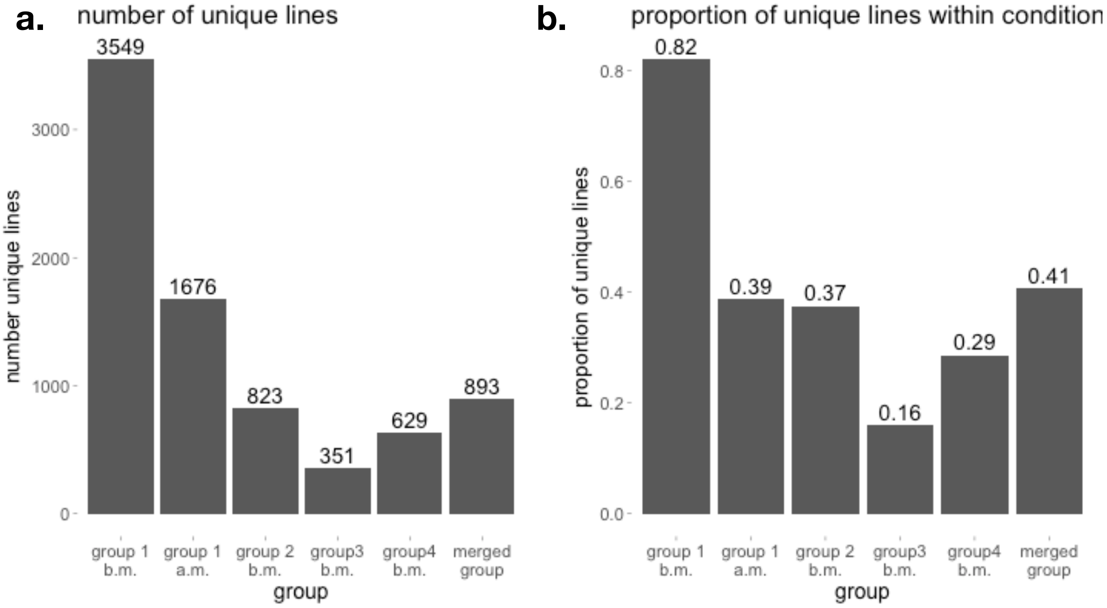


Figure 5.14 – (a) number of unique lines and (b) number of unique lines as a proportion of the total number of unique lines in each of the two conditions (large group vs. merged group), for all groups, before and after the merge

5.3.4.2. Does splitting the population into groups increase diversity?

While the small groups separately were less diverse than the big group, it could be the case that once the three small groups are pooled together, this pooled diversity is actually larger than the large group diversity, because the three small groups in fact introduce different solutions. This would answer the question of whether splitting groups generates more diversity overall.

This did not seem to be the case - the diversities in the large group and the small group pooled were comparable (Fig. 5.15). While in absolute numbers, the diversity in the large group was almost twice as high as the diversity in the pooled small groups (Fig. 5.15a), the diversities were practically equal when controlling for the total number of lines submitted in each condition (Fig. 5.15b). This suggests that, although the diversity within each small group was relatively small, the solutions in these small groups were different enough that, once pooled together, the diversity reached levels comparable to the large group. Indeed, while the small groups 2, 3, and 4 introduced 823, 351, and 629 lines each before merge, the overlap between these groups in terms of lines was minuscule. Groups 2 and 3 had 12 lines in common, groups 2 and 4 had 15 lines in common, and groups 3 and 4 had 10 lines in common. This indicates that each group converged on its own group-specific solutions, with little common ground between groups. There was similarly little overlap between the lines in the large group and each of the small groups, suggesting again that each groups converged on its own solution 'tradition', with little similarity across groups.

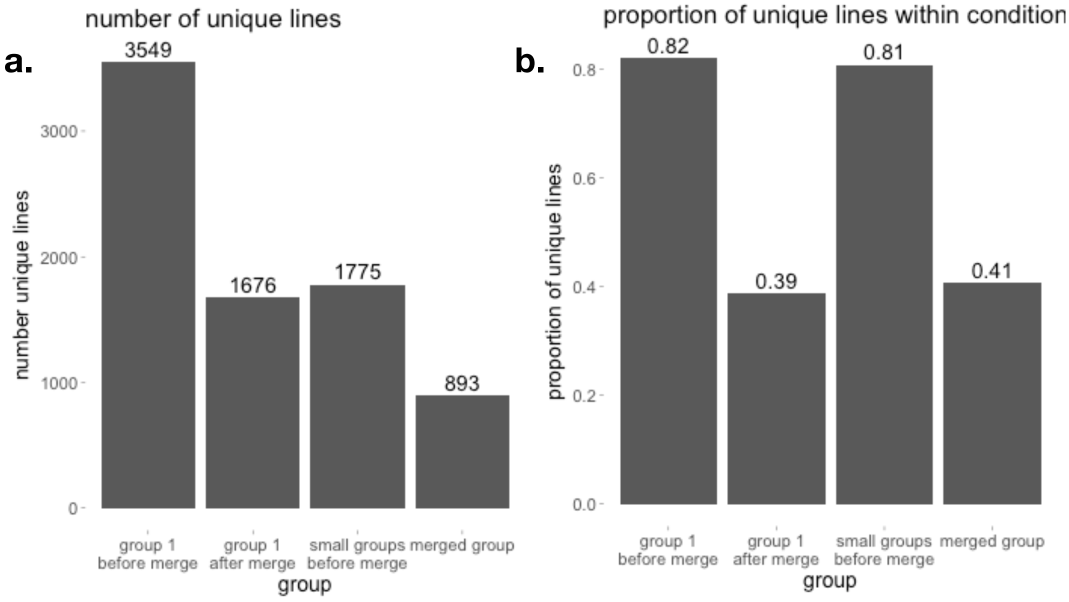


Figure 5.15 – (a) number of unique lines and (b) number of unique lines as a proportion of the total number of unique lines in each of the two conditions (large group vs. merged group), for the large group before and after the merge*, the three small groups pooled before merge*, and the merged group

5.3.4.3. Does diversity decrease after merge?

If the convergence in the large group were strong enough, and the players in the merged group pool together their solutions after merge, we would expect that the diversity in the large group would be smaller than the diversity in the merged group (after the merge). This was not the case (Fig. 5.15) – the diversity in both conditions after the merge date was comparable once we controlled for the total number of entries submitted.

In fact, after the merge date, there were two distinct processes at work in the two conditions, responsible for the diversity patterns witnessed. Figure 5.10 clearly illustrates that in the large group the population converged on a specific solution and maintained that solution throughout the whole last three days of the contest, after merge. In the merged condition, however, it was not the case that the population adopted any of the solutions already existing in any of the 3 small groups prior merging. The moderate similarity within the merged group suggests the population was working on a relatively consistent solution that persisted in the group (Fig. 5.11f), but this solution was not based on any previous solution originating in any of the small groups before merge as the code similarities indicate. It was, in fact, a new solution that the group created after the merge. Therefore, although the diversities in the large group and the merged group were comparable, they were the result of two different phenomena. In the large group, the diversity decreased as a result of convergence on a similar solution, while in the merged group the diversity decreased as a result of the introduction of a new solution unlike those in any of the smaller groups beforehand.

5.3.4.4. How does diversity change over time?

In order to illustrate how diversity changed over time within condition, I split the diversity presented in Fig. 5.14b across conditions by day. Therefore Figure 5.16 plots the number of unique lines in each group per day, presented as a proportion of the total number of lines introduced in each of the two conditions, large group vs. merge group. There was a general downward trend in the large group, though the last day displays more diversity, driven by last minute competition. The diversity did not change in such an evident way in the small groups. Group 2 showed a relative increase, followed by a decrease in diversity over the first four days of the contest, while groups 3 and 4 were characterised by less activity, but a decreasing trend in diversity. Finally, when the groups were merged the diversity soared, but decreased by the end of the contest. Therefore merging the small groups seems to have increased the diversity, but bear in mind that if the small groups are pooled together, we actually observe a change from a much larger pooled diversity, to reduced diversity once the groups merged (Fig. 5.15).

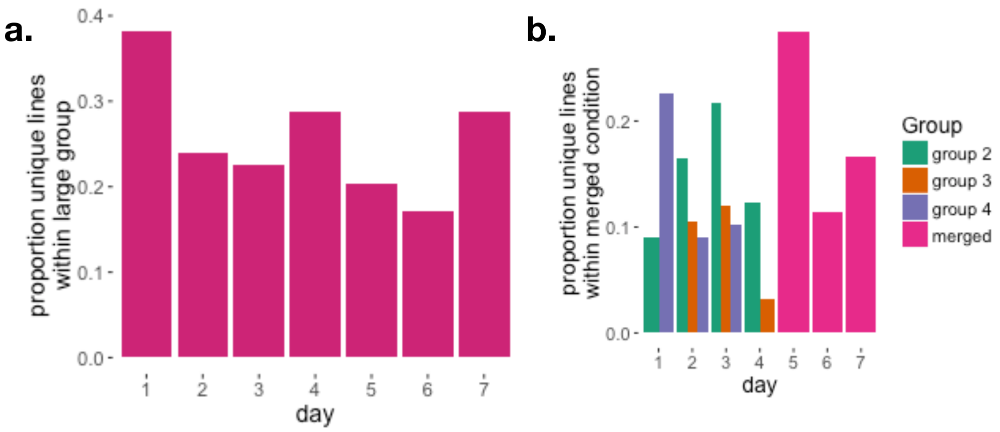


Figure 5.16 – (a) diversity measured as the number of unique lines submitted per day in the large group, presented as a proportion of the total number of unique lines introduced in the large group overall, for ease of comparison between conditions. (b) diversity measured as the number of unique lines submitted per day in the merge conditions, as a proportion of the total number of unique lines introduced in the three groups before merge and in the merged group

The relationship between cultural diversity and the time measured in equal-sized intervals as discussed in the Methods for each of the 5 groups are presented in Figure 5.17. Some of the groups are characterised by fewer than 10 data points because there were no entries submitted in some of the time intervals. There was relatively large variation in how diversity changed between groups. While there was a general negative trend in the relationship between time and diversity, group 2, for example, actually showed a positive relationship. However, time and diversity were not significantly correlated for any of the groups, therefore there was no consistent diversity change over time that could be picked up at the group level.

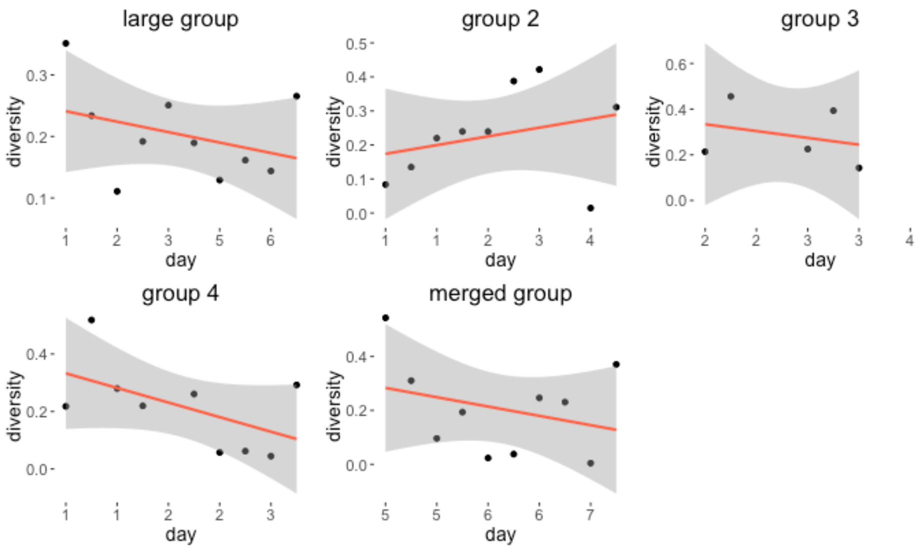


Figure 5.17 – diversity measured as the proportion of unique lines out of the total number of lines submitted within each group, per time interval for each group

Comparing the change in diversity between conditions throughout the entire week shows a clear difference (Fig. 5.18). There was an obvious downward trend in the merged group condition, but the relationship between cultural diversity and time in the large condition was not as obvious. Indeed, results from the linear model showed that time was not a significant predictor of the change in diversity in the large group, but it was in the merged group condition (Table 5.5). This is most plausibly due to the fact that diversity in the large group at the end of the contest increased as a result of increased competition, which was associated with more novelty. Excluding the last day of the contest, the trend is clear in both conditions, suggesting that, again, diversity decreased over time as players introduce less novelty and focus instead on developing entries based on previously submitted entries.

	Time estimate	Std. Error	t-value	p-value
Large group *diversity ~ time interval*	**0.01**	**0.021**	**0.49**	**0.627**
		F(1,18) = 0.243, R2 = 0.013		
Merged group *diversity ~ time interval*	**-0.066**	**0.027**	**-2.44**	**0.024***
		F(1,18) = 0.249, R2 = 0.249		

Table 5.5 – results from the linear model diversity ~ time interval for the data in the two group conditions

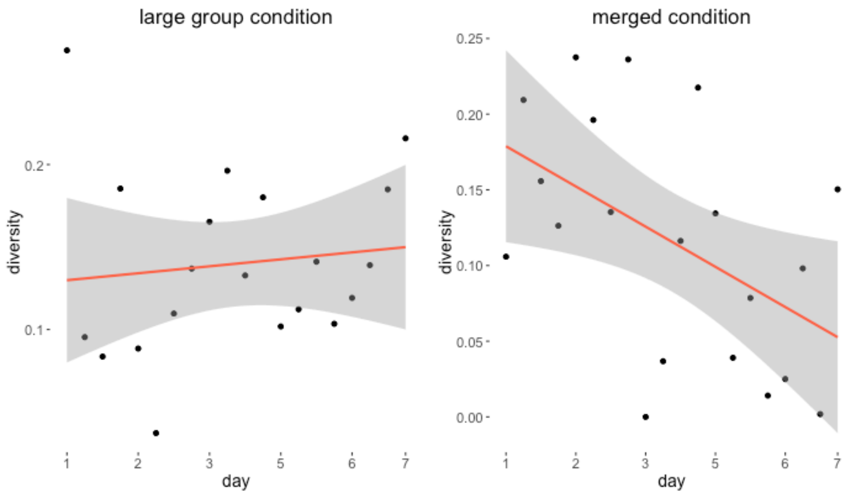


Figure 5.18 – diversity measured as the proportion of unique lines out of the total number of lines submitted within each condition, per time interval for each condition

5.4. Discussion

This chapter set out to test whether manipulating group structure affects cultural diversity and performance in the programming contests paradigm. In the large group condition participants showed more activity above and beyond that expected by the difference in the number of players between that and the other smaller groups. Out results suggest an interaction between group size, competition, and individual variation, which affects diversity.

In terms of performance, the large group was associated with a higher overall improvement, characterised by many small incremental steps. The experimental small-group condition achieved less improvement, but through fewer, larger advances. The incremental nature of improvement is not surprising under the stronger competitive regime expected in the bigger group. Improvements are harder under the given time constraints, when there is a higher possibility that a different individual could 'scoop' your idea. The convergence in solutions would also promote more incremental improvements, since Chapter 3 showed that higher entry similarity translates into smaller score variation. It could even be the case that stronger competition and time constraints drive the population towards stronger convergence, as copying is a less risky strategy in a competitive context than the independent invention of solutions.

In the first half of the contest, entries in the large group in fact were characterised by worse average performance compared to the merged condition, because of higher variation in score at the beginning of the contest. This raises interesting questions regarding the link between exploratory behaviour, variation, and performance, and relates to results presented in the Chapter 4, where I showed that more exploratory individuals performed better overall in the context of the previous programming competitions. Because there is no cost to submitting a poorly performing entry as a means of testing an algorithm, for example, it may be the case that here, too, the individuals who explore the problem more and submit more varied entries manage to achieve superior solutions that score better. Why this behaviour would be more prevalent in the large group remains an open question, but it could tie in with differential motivational patterns between the two conditions.

It is less clear whether the lack of activity we witness in the small groups relative to the large group is merely an artefact of the small sample size in this experiment (two of the small groups consisted of only 3 and 5 active players), or whether it could be a genuine mechanism that underlies the relationship between group size and cultural complexity in real world data. There is evidence that performance cues promote exploratory behaviour and increase performance (Toelch *et al.*, 2011). Using a computer-based task allowing for innovations of varying degrees of difficulty, which also vary in their payoffs, the authors tested whether participants varied in their exploratory behaviour and performance when they were exposed to different performance cues. They framed the performance cues in terms of the previous participants' scores, which they presented to participants. Results show that participants cued with low scores showed a drastic reduction compared to participants cued with high scores, both in terms of exploratory behaviour and innovations discovered, as well as overall performance.

This mechanism could be solely responsible for the differences we see in performance between groups in our data. If knowing that other individuals are performing better is enough incentive to explore, innovate, and improve, then it could be that the lack of those social cues is enough to stifle exploration and cap performance to a standard deemed acceptable in the absence of contradictory information. This would mean that in a functional task, once the group grows enough that there are enough individuals to provide social cues regarding performance, social comparison would then drive individuals to become more exploratory and start improving substantially, which will in turn encourage even more exploration and improvement. The relationship between group size and cultural complexity could be purely a matter of the interplay between social cues and competition. Current models investigating group size like Henrich's (Henrich, 2004) typically assume the free exchange of information and further theoretical work incorporating groups structure and varying group sizes should help elucidate whether the phenomenon proposed here does play an important role in cumulative culture. Furthermore, while theoretical models typically assume equilibrium has been reached, in the case of the MATLAB contest the problems allow for open-ended advances in skill. Improvement becomes increasingly and drastically difficult over time, but it is possible at any point in time. A week was chosen for the duration of the experiment here mainly for practical reasons and because improvements seemed to level out after this period in previous contests, but it could be the case that in theory the dynamics observed here would change if we allowed the experiment to run ad infinitum. Clearly, the unfeasibility of such a study constrains our experimental approach, but further theoretical work could help elucidate these questions.

An alternative, or perhaps complementary, explanation for the differential patterns of activity and performance witnessed could simply be that individual identity interacts strongly with the different competition modes in the two conditions, which exacerbates these differences. Two participants in the large group who contributed a disproportionately large number of entries also proved to be two of the best players in the entire competition. It could be, then, that this increased performance in the large group is the result of an interaction between players' abilities, the initial diversity of solutions contributed by more individuals in the initial days of the contest, and increased competition, which could in turn also be strongly affected by activity and diversity of solution. It remains unclear, then, whether this result is purely due to individual-level characteristics, population dynamics, or due to an interplay between the two.

With regards to similarity and novelty, the large group displayed the same convergence of solutions and 'tweaks and leaps' dynamic observed in previous contests, while this pattern was ambiguous at best in the small groups. The merged condition showed more novelty both before and after the merge. While the entries in the large group showed high similarity to the current leader, the pattern was reversed in the small groups, in which entries did not resemble the current leader much, suggesting that payoff bias was very strong in the large group, but largely absent from the small groups. Nonetheless, when entries did copy the current leader in both conditions, it paid off – there was a positive relationship between improvement and similarity to the current leader in both conditions.

Finally, the large group was characterised by a more diverse repertoire in terms of the number of lines of code used in individual solutions, and generally by longer solutions, indicative of a larger, more complex cultural toolkit. This is in line with much of the evidence surrounding the debate regarding population size and cultural complexity discussed in the introduction. I found clear evidence that a larger population sustains a larger cultural repertoire, but it is worth bearing in mind that the number of individuals present in these groups is considerably smaller than what we would expect real populations to consist of. The real-world populations from Oceania discussed in Kline and Boyd, for example, amount to thousands of individuals (Kline and Boyd, 2010), while some of the groups in this experiment only contained 3 or 5 individuals. In this sense, the results here are more easily comparable to experimental studies of group size and cultural accumulation like the ones performed by Derex et al. (2013) or Muthukrishna et al. (2013).

However, it is unclear whether cultural accumulation undergoes a qualitative difference once groups increase in two or three orders of magnitude. It could be that group size has a very strong effect on cultural improvement for small groups, but once the population grows into the order of thousands of individuals, these differences in improvement become less prominent. A possible explanation could tie in to the effect of group structure on cumulative culture: small, well-connected groups promote fast accumulation, and a difference between the collective knowledge of 5 vs. 10 individuals evidently affects how the group improves in skill, while in large groups information travels slower, which would hinder the effect of increasing population size. The sample size in our experiment therefore means we investigated a ‘small group effect’, where an increase in group size from 5 to 20 individuals translates into a noticeable increase in the cultural toolkit.

Returning to the hypotheses proposed in the introduction, we expected that larger groups would entertain more diversity. Indeed, even when controlling for the size of the repertoire, the smaller groups showed less diversity than the larger group. We also hypothesised that splitting individuals into groups should generate more diversity, and this diversity should relate to higher improvement overall. When pooled together, however, the diversity of the small groups combined was similar to the diversity of the large group, indicating that dividing the population in groups did not increase, nor decrease, the cultural diversity in this case. If anything, results showed the opposite pattern to that expected – the diversity in the pooled group was comparable to the diversity in the large group, but the population-level performance in the latter was better, both at the merge date and overall throughout the whole contest.

The diversity of solutions decreased in both conditions over time, but through different mechanisms. On the one hand, the large group converged on one solution that became established in the population through copying. On the other hand, the three small groups each entertained different solutions. All of the groups showed different 'traditions' in terms of the solutions they each entertained, as there was little overlap between the code used in either of the groups.

This evidence for different processes affecting the dynamics of cultural diversity could explain the surprising result regarding the lack of increased performance in the merged group condition. We assumed that the tweak and leap dynamic would be present in both conditions – populations would converge on the most successful solutions, therefore multiple groups would converge on a more diverse set of solutions, which would promote increased improvement. Instead, there was little convergence in the small groups, which might be the result group size in the small groups. The distinction in cumulative culture regimes we made above between groups of 5 or 10 individuals and groups of thousands of individuals could be applied here as well. Thus, a large group of, here, 20 individuals (but up to 200 in the previous contests presented in Chapters 3-4) creates a strong competitive system characterised by fast initial improvement, in which copying is a much cheaper alternative to individual learning. A small group, such as in our small group condition here, does not. Instead, individuals rely more on individual exploration, which has drastically different effects on the dynamics of both culture and skill improvement.

Naturally, the generality of these results is dependent on our experimental approach. I designed the experiment expecting bigger sample sizes (along the lines of 50 and 10 participants in the large group and the small group, respectively), which were not achieved. Whether the results presented here regarding differential cultural diversity dynamics in the different sized groups still hold with larger sample sizes is an open question. It is very possible that, as predicted, slightly larger groups will develop the tweak-and-leap dynamic. Then, group size could remain a modulator of performance when both small and large groups show the same cultural diversity dynamics, or it could be that the patterns of improvement prove to be drastically different – further work will disambiguate this. An obvious future experiment already being planned will try to attract more participation and more activity by using a more competitive reward (perhaps prize money). Nonetheless, this complication emphasises the importance of taking sample size into account when interpreting experimental results from studies interested in group size.

Therefore, this work did not find evidence for group structure as a driver of cumulative improvement via increased cultural diversity per se, but it added evidence for another layer of complexity to the debate regarding the importance of population size on cumulative culture by finding a qualitative difference in the dynamics of cultural evolution between groups of different sizes. Whether this qualitative difference is the result of differential competition regimes, individual abilities, cognitive mechanisms underlying motivational differences, populations dynamics, or an interplay between all these factors, remains an open question.

Chapter 6

Discussion

6.1. Summary of findings

This thesis has been generally concerned with the drivers and dynamics of cumulative culture, analysed in novel, more naturalistic settings than ever before. In Chapter 2 I used a complex agent-based model to investigate how cumulative improvements, termed refinement, interact with the trade-off between social and individual learning in the Social Learning Strategies Tournament. I found that, in the tournament context, refinement leads to tensions between individual and population interests, as the population benefits from a higher refinement rate than is individually beneficial. Through refinement, strategies could construct a more beneficial environment in which refined behaviours are the most advantageous, but to this end strategies had to pay a cost for refinement, which led to differential success outcomes for strategies that did use refine relative to strategies that did not. Copying allowed individuals to attain refinement without paying this cost, and led to a strong convergence in the population on a small number of refined behaviours.

This pattern of convergence was confirmed experimentally with human data in Chapter 3 using the MATLAB programming competition as a model of real-world cumulative culture. We have shown that, in a cumulative setting, improvement in a task quickly became extremely difficult. Innovation was a risky strategy, as it was associated with large rewards but, more often than not, it led to notable failures, while copying was safe and was associated with a small score variance. This drove individuals to primarily engage in tweaking behaviour by copying and modifying the best-scoring solutions, and comparatively little innovation – this pattern is well recognised in the economics literature (Lane, 2016). As a result, solutions increased in similarity over time, which caused a concurrent and drastic decrease in cultural diversity, as the population converged on extremely similar solutions. Individuals mostly relied on copying as a way of acquiring solutions – innovation and recombination were rare at the individual level, but recombination of cultural traits accumulated at the population level as a result of considerable persistence of old ideas over time.

Chapter 4 addressed the question of individual differences in engaging in copying and innovation in a cumulative culture setting, again using the MATLAB contests as a model. I found that individuals varied widely in their preferences for social or asocial learning, but that the best performing individuals introduced less novelty overall while at the same time showing more exploratory behaviour in terms of the similarity of their solutions to the current leader. Individual differences in performance contributed to establishing reputations within and across contests, which lead to prestige effects, as individuals who submitted leading entries had higher influence on subsequent solutions overall. Neither population size, nor participant composition seemed to affect improvement throughout the contest. Therefore, while variation was beneficial at the individual level in terms of the novelty of solutions, it did not seem to have an effect at the contest level.

Finally, in Chapter 5 I experimentally investigated whether group structure can affect cultural diversity, and therefore the dynamics of improvement and similarity using the MATLAB contest paradigm. I showed that a larger participating group was linked to larger overall improvement, characterised by more, smaller increments, while smaller groups achieved worse overall performance. The two group structure conditions showed differential patterns of cultural diversity. The large group converged on similar solutions through copying, replicating results from Chapter 3. However, the three small groups each entertained independent solutions, and once merged they converged on a separate common solution. This means that in both conditions the cultural diversity decreased over time, but through different processes.

6.2. Broader implications

A common theme emerging from Chapters 2 and 3 is that cumulative culture can lead to a dramatic collapse in diversity. Cumulative culture creates a scenario in which a great deal of investment in terms of time and effort goes into improving a particular solution, which becomes remarkably more efficient than any one individual could every recreate in their own lifetime (or contest participation, in the case of the MATLAB contest). Thus copying is a cheaper and much more efficient alternative to trial-and-error learning, and as a result the population convergences on the same solutions through social learning. This was the case for the Social Learning Strategies Tournament, where individuals had a choice between a number of discrete behaviours that can be improved sequentially, but also in the open-ended case of the MATLAB contest, where individuals were free to develop any solution to the problem. What we saw was that, even in such an unconstrained environment, individuals still converged on similar solutions through copying. This convergence translated into a drastic decrease in cultural diversity.

This result creates a paradox, as this lack of diversity is not something we observe in real human culture globally. Cumulative culture has been proposed to be the key process that explains the uniqueness of human culture, but in these contexts it led to opposite patterns to what human culture is characterised by. There are several possible explanations that are not mutually exclusive. One possibility is that payoff bias is key for explaining our results in both cases, yet in the real world we do not expect individuals to always be able to accurately assess how useful a skill or solution would be. We expect that if the link between a behaviour and its payoff is blurred, one lacks a reliable way of measuring which behaviours are useful, which may break down this pattern of convergence we witness. That may not necessarily be the case, though, since individuals could adopt other heuristics that would allow them to acquire beneficial behaviours, like attending to characteristics pertaining to individuals, if those characteristics can systematically be linked to possessing good skills. Prestige bias would be an example of this (Henrich and Gil-White, 2001), which when used sensibly by the population could lead to the same convergence patterns we see in our results. Indeed, my results indicate evidence of a prestige-type effect even when the payoffs are easily accessible, and this effect is strong enough to persist even when controlling for individual performance. This suggests that payoff bias and prestige bias are not mutually exclusive strategies, but can co-exist. Therefore it would not be implausible to believe that were the strength of the payoff bias manipulated through decreasing the transparency of the outcomes, the population would lean more strongly on prestige bias.

Another reason for the lack of diversity witnessed could be related to the fact that in this work I focused on specific processes at work in cumulative culture. The tournament was concerned with refinement, or incrementally improving a single trait, while the MATLAB contest employed a highly replicative mechanism, where individuals could copy verbatim other solutions. Different processes can lead to different patterns of evolution and diversity at the population level (Enquist, Ghirlanda and Eriksson, 2011), so it is important to identify which mechanisms support cumulative improvement in which situation. Naturally, we should not imagine that culture evolves following simple, clear-cut patterns – rather, several mechanisms would be at work at the same time, which would explain why the patterns of cultural diversity witnessed in the real world are more complex than what this work illustrated. Importantly, whether cumulative evolution relies more heavily on incremental modifications than big jumps, for example, is expected to be domain dependant (Acerbi and Mesoudi, 2015). We would not be surprised if in a functional domain like tool making, where the effectiveness of a tool is highly dependant on following a correct design sequence and where failing to do so can mean the difference between starving or surviving, there is strong pressure for high replicability. In such a domain, one would want to copy a useful design as accurately as possible to ensure success. Other domains, like symbolic culture, are subject to different pressures, and perhaps rely on different innovative processes. It is not functionality, but converging and maintaining group markers, for example, that affect how cultural traits are learned and change over time in this case.

Additionally, while these cultural dynamics in respect of single, encapsulated problems like the programming contests would generate the convergence witnessed here, cultural diversity might emerge from the diversity of cultural traits in different domains observed in entire populations, and ecological diversity that can provide new problems for cumulative culture to solve. Similarly, the empirical studies presented here are mostly concerned with a single group per trait, while meta-populations of unrelated subgroups would most likely involve different traditions or solutions to even similar problems. We expect that different populations would be characterised by varying numbers of domains, which themselves vary across ecological contexts, thereby raising diversity levels.

Therefore the choice of defining ‘cumulative culture’ in the modelling and experimental work will crucially affect the results. The theoretical literature has modelled cumulative culture in a variety of ways, from the mere persistence of a trait in the population (Enquist and Ghirlanda, 2007; Enquist *et al.*, 2010), to an increase in the number of traits (Enquist *et al.*, 2008; Strimling *et al.*, 2009), continuous or sequential improvement in a single trait (Henrich, 2004; Mesoudi, 2011c; Nakahashi, 2014), or an infinite number of traits being invented in a fixed sequence, each with an infinite number of complexity levels (Kempe, Lycett and Mesoudi, 2014). The experimental literature has conceptualised cumulative culture as improvement in a skill like building a paper airplane (Caldwell and Millen, 2008, 2010), tying a knot (Muthukrishna *et al.*, 2013), or more ecologically valid tasks like building fishing nets or arrowheads (Derex *et al.*, 2013, 2015). As mentioned earlier, one modelling study proposes a more complex cultural system in which traits interact, facilitate and inhibit each other (Enquist, Ghirlanda and Eriksson, 2011), but this proposal of increasing the complexity of the modelling approaches for cumulative culture has not been taken up by future studies. Similarly, in a recent experimental study, Derex and Boyd (2016) go beyond viewing cumulative culture as a liner increase in a skill, and incorporate recombinations as the central driving force of improvement.

All of these studies understandably implement artificial simplifications of a large-scale complicated process that operates in large populations over impractical timescales, in order to gain insight into some of the mechanisms involved in cumulative culture, and we have done the same in the Social Learning Strategies Tournament presented in Chapter 2. The type of refinement implemented in this work is clearly not full-blown cumulative culture as it relies on sequentially improving independent traits, but it nonetheless considerably increases our understanding of the type of culture that can allow a population to overcome environmental variability. None of the previous studies have attempted to investigate refinement using agent-based simulations which enable us to follow how individual-level decisions translate into population outcomes, in a large interactive changing environment, and it is precisely this paradigm which allowed us to show how individual learning can lead to population-level convergence of cultural traits.

The MATLAB contests provide what arguably is the most realistic empirical model system of cumulative culture to date in the literature. A large group of individuals is collectively solving a difficult challenge within the confines of a complex programming language while openly sharing their solutions and the payoffs. The way participants craft solutions reflects how real-world innovation takes place, through copying, modification, and recombination, which lets us directly asses the benefits of different individual social learning strategies, as well as their effect on the population patterns of improvement and cultural change. Admittedly, this took place on a limited time scale of one week, with a smaller population that what is observed in the real world, but it provides a tractable framework for answering questions regarding cumulative culture in an experimental setting.

The MATLAB programming contest provides real-world evidence on how collective improvement takes place in a technological domain. The patterns of improvement showed strong reliance on tweaking the current best solution, but also rare maverick innovations that make large improvements. Technological improvement generally shows a pattern of incremental improvement in which technologies change in small steps towards more optimal designs (Basalla, 1988), but the history of technology and science has usually glorified individual ‘lone geniuses’ as the drivers of progress. In a reaction to this, recent work has been focusing on the idea that collective improvement depends very little on individual-level inventive abilities, but rather on a ‘collective brain’ type effect in which individuals cohabitate and cooperate as a result of evolved norm-psychological pro-social processes and cooperative institutions. In large-scale societies small incremental improvements accumulate until a critical mass of small innovations is reached, which gives rise to what appears to be a completely novel invention that in fact relies on recombining and modifying already existing cultural traits (Henrich, 2016; Muthukrishna and Henrich, 2016). Muthukrishna and Henrich (2016) propose that the main types of innovation are recombination and refinement – the only individual-level type of novel invention they recognise is serendipity, where individuals accidentally discover a beneficial trait, but entirely discard the possibility that individuals could introduce extremely novel inventions. However, here I have shown evidence for both incremental improvement and large beneficial innovations.

In the MATLAB contests there was little evidence of recombination at the individual level, with the main mode of technological improvement being refinement. Nonetheless, I also found clear evidence of entirely novel solutions that make large increases in the overall performance. The ultimate source of these innovations is unclear since we do not know what causes specific individuals to introduce novel beneficial solutions, but there is little debate that individual abilities should be a key factor – some individuals are more skilled and manage to invent a new, better solution. Whether this solution is ultimately inspired by previous ones, or by other programming problems outside of the MATLAB domain, is rather a philosophical issue – how large is the domain that recombinations draw from, how far back in time do we track modifications, how do we define serendipity? What is less arguable is that in the context of these programming contests, collective improvement did take place both through tweaks and leaps.

If, like Henrich and Muthukrishna (2016), we assume that cumulative improvement relies on recombination and refinement, then clearly the population size should directly affect the rate of improvement. The more individuals in a population, the higher the variation of cultural traits that could potentially be combined or refined, which would lead to higher diversification and, implicitly, higher improvement. This is the key assumption in the Henrich model of Tasmanian cultural loss (2004) and much of the work investigating the importance of population size to cultural complexity. This thesis brings mixed evidence for the effect of group size on cumulative culture. In Chapter 5 I showed that larger groups were characterised by a larger toolkit associated with higher overall improvement, but in Chapter 4 I found no link between population size and improvement across contests. This is consistent with the controversy in the modelling, experimental, and field study literature – while experimental work focusing on small group sizes consistently found that an increase in the group size promotes more improvement, studies on real populations sometimes do (Kline and Boyd, 2010; Collard, Ruttle, *et al.*, 2013), and sometimes do not (Collard, Kemery and Banks, 2005; Collard, Buchanan, *et al.*, 2013) find this effect.

However, Andersson and Törnberg (2016) built on the Henrich model to relax the copy-the-best assumption by incorporating a parameter that controls the strength of the skill bias, and by adding a dependency between skill complexity and imitation errors. Thus, in their model, the authors could investigate the relationship between population size, skill bias strength, and imitation fidelity. Allowing imitation errors to depend on the complexity of the skill essentially puts a cap on how much a population can improve in skill through a trade-off between selection pushing for higher skill complexity, and the maladaptive nature of transmission errors. Even more, they found that, when the fidelity of transmission is kept constant, increasing population size increases skill complexity for small population sizes (in the order of a few tens of individuals), but does not increase complexity for large population sizes. Results from this thesis seem to confirm that this relationship between group size and cultural complexity may be non-linear, such that the effect of increasing group size diminishes as the population increases. Even more, this relationship might vary across cultural domains (Lupyan and Dale, 2010; Acerbi, Kendal and Tehrani, 2017), such that we might expect that a technological domain would show a stronger relationship between population size and cultural complexity.

6.3. Current debates in cultural evolution

The convergence illustrated both through theoretical and experimental approaches in this work provides valuable insight into the issue of conformity, as it shows that when individuals make sensible decisions in a cumulative cultural setting, behavioural homogeneity can be achieved without having to resort to complex cognitive mechanisms such as normative conformity. This conformist bias, defined as disproportionately copying the majority, has been suggested as a key mechanism that can ensure between-group differences, which is necessary for cultural group selection to operate on (Boyd and Richerson, 1985; Henrich and Boyd, 1998). Cultural group selection is an important candidate theory for explaining the evolution of large-scale cooperation in humans. If there is variation in co-operative tendencies between individuals, and these co-operative tendencies stabilise at the group level through a mechanism like conformity, then if we assume that co-operative groups are more successful than non-co-operative groups, selection would increase the frequency of co-operation at the meta-population level (Boyd and Richerson, 1985). This theory has sparked much interest in the evolution of a conformist bias in both humans and non-human animals, but evidence is debateable (Eriksson, Enquist and Ghirlanda, 2007; Efferson *et al.*, 2008; Morgan *et al.*, 2012; van Leeuwen and Haun, 2014), and depends to a large extent on how each study defines conformity (van de Waal, Claidière and Whiten, 2013; Aplin *et al.*, 2014).

Normative conformity, for example, has been well studied by the psychology literature ever since the 1950s (Asch, 1956; Bond and Smith, 1996), but whether naïve individuals indeed disproportionately copy the majority, as the cultural evolution literature suggests, has only been confirmed in one study (Morgan *et al.*, 2012). Even more, when given a choice between using a payoff bias or a frequency-dependant bias, people seem to prefer the former, so it is still unclear under which circumstances a conformist bias would be beneficial (McElreath *et al.*, 2008; Mesoudi, 2011a). A more recent study has incorporated cumulative culture in explaining large-scale co-operation through group selection by positing that cumulative culture has sparked a complex of cognitive adaptations including improved social learning and conformity that support co-operation, which spread through group selection and increase selection for pro-sociality (Chudek and Henrich, 2011). My analysis from Chapters 2 and 3 suggest that a conformity bias is not necessary to promote the behavioural homogeneity necessary for cultural group selection to operate on, but instead cumulative culture creates a pressure for increased copying, which leads to convergence and conformist outcomes.

The domain-specificity of cultural evolution dynamics ties in with recent suggestions of a potential need to extend models of the replicative nature of culture to incorporate more specific cognitive mechanisms involved in the transmission of culture. Cultural attraction theory has drawn attention and, sometimes, criticism, by arguing that the cultural evolution field has been focusing too much on the replicative nature of cultural transmission (Claidière, Scott-Phillips and Sperber, 2014; Acerbi and Mesoudi, 2015; Morin, 2015, 2016; Sterelny, 2017). Cultural attractor theorists suggest that culture is not copied faithfully from one individual to another, but rather each individual reconstructs each cultural trait every time they learn it. Cultural transmission, then, is not purely a selective process where individuals choose 'intelligently' between different variants, with those variants copied exactly. Rather, in this view culture becomes a transformative process in which individual cognition becomes crucially important. The main idea is that the stability of culture is explained by the fact that individuals possess certain "cultural attractors", which determine which information is preferentially maintained, and which guide changes in cultural traits towards these attractors (Claidière, Scott-Phillips and Sperber, 2014).

This observation is supported by experimental studies using transmission chain experiments, in which participants are required to remember and pass on short vignettes, showing that people display several biases with regards to the retention and distortion of such vignettes. People preferentially remember features concerning social information and survival information (Mesoudi, Whiten and Dunbar, 2006; Stubbersfield, Tehrani and Flynn, 2015), as well as emotionally arousing content such as disgust (Stubbersfield, Tehrani and Flynn, 2017), and participants even sometimes transform the stories so that they become more consistent with these biases. A particularly convincing study presented participants with a novel artificial system of colour terms paired with real colours, and asked them to generalise the labels learned to new colours. Results showed that through an iterated learning paradigm, over simulated generations, people converged on colour systems very similar to colour systems seen across natural languages, as guided by their individual perception biases (Xu, Dowman and Griffiths, 2013).

Some have argued that this reconstructive position is not different from Boyd and Richerson's 'guided variation' process, in which individuals not only copy traits, but also modify them as part of the transmission process (Acerbi and Mesoudi, 2015). This view, however, has not constituted the main focus of the cultural evolution literature, and cultural attraction theorists claim that in fact this is the main mode of transmission at work in cultural evolution, which shifts the emphasis from emerging collective innovations to individual cognition (Boyd and Richerson, 1985; Laland, 2004; Rendell *et al.*, 2010; Henrich, 2016; Muthukrishna and Henrich, 2016).

Acerbi and Mesoudi (2015) argue that the reliance on either reconstructive or replicative processes depends on the cultural domain. As mentioned above, we expect that causally opaque technologies require stronger preservation and hence favour replicative processes, while domains like the colour systems discussed above will be more strongly influenced by perceptual attractors. Cultural attraction theory is most interested in explaining why traditions with no obvious utilitarian purpose, like songs and folk tales, persist over time, and seems to be better suited for case-by-case proximate explanations of cultural change, while the classic view of cultural evolution seems to be more interested in ultimate questions. This domain dependency and the difference in the relevant mechanisms supporting cultural stability in different domains is important when interpreting already established findings. Acerbi, Kendal, and Tehrani (2016) find, for example, mixed results in the relationship between population size and cultural complexity in the domain of folktales. These results are mediated by the metric they use to measure complexity, and the authors argue that this relationship with population size may be less relevant in folktales than in a domain like technology precisely because of their differential reliance on reconstructive processes.

Finally, contrasting cultural attractor theory to the classic view of cultural evolution asks which factors are more important when explaining cultural stability – cognitive transformations, or the interaction of individual decision-making processes and population dynamics? The answer is probably in the middle, with attraction and selection representing two ends of a continuum on which the relative importance of preservative or reconstructive processes is an empirical question. Sterelny (2017) argues that if we can overcome methodological challenges and compare the two positions, it could either be the case that 1) populations of trusting and discerning social learners lead to the same dynamics, 2) cumulative culture would be rare in a population of discerning social learners, because incremental improvement relies on faithfully copying causally opaque skills, or 3) discriminating social learning might actually lead to better cumulative adaptation, as individuals would generate more useful innovations. Ultimately, whether there are significant qualitative differences between the two approaches and their effect on cumulative culture remains an empirical question.

Nonetheless, cultural attractor theory argues that cognition should be a stronger focus of the cultural evolution field, and this idea is not new (Heyes, 2012a, 2012b; Heyes and Pearce, 2015). Heyes thinks that the cultural evolution field has relied on behaviourist approaches to social learning and cannot say much about the cognitive mechanisms at work in social learning, nor their neurological underpinnings (Heyes, 2012b). For example, in a critique of social learning strategies, the author points out that the literature sometimes addresses these social learning strategies as if they are genetically specified adaptations for cultural learning, but they could very well be relying on the same cognitive mechanisms as asocial learning. The ‘social’ in social learning could just be the fact that, in the case of social learning, the input mechanisms are biased to preferentially attend to social cues (Heyes, 2012a).

A comprehensive understanding of social learning should, naturally, include cognitive explanations, but a focus on how social learning works mechanistically could also shed light on how and why individual differences in social learning arise (Molleman, van den Berg and Weissing, 2014). In addition to consistent individual differences in social learning, we have evidence of different social learning approaches across cultures (Mesoudi *et al.*, 2015; Glowacki and Molleman, 2017). I expect that the evolution of these cultural differences would be mediated by group structure (as I have shown in Chapter 5 that different groups converge on different cultural traits) but, more importantly, it would be supported by the fact that cultural learning itself can be culturally learned (Heyes, 2012a). Heyes suggests that the psychological processes that make cultural learning possible are not genetic adaptations, but rather learned in development through social interactions. If the way we use social learning is learned socially, then clearly the culture we grow up in will affect our approaches to social learning, which will lead to these cultural differences we witness. Therefore using the “broad brushstroke” work done so far to guide more specific studies of cultural variation and individual cognition would have important consequences for explaining human culture.

This recent debate surrounding cultural attractors emphasises the fact that in this work we have defined cumulative culture in a narrow sense, focusing mainly on incremental improvement in technology. This has indeed been the main target of the classical view of cultural evolution (Henrich, 2016; Clarke and Heyes, 2017), and stems from an initial interest in understanding the adaptive value of culture. If we think that culture was shaped by natural selection, the natural initial focus should rest on functional culture that has direct fitness benefits, so technology is a logical place to start to investigate the emergence of culture. However, as discussed above, different cultural domains are under different pressures, so it is unclear how results from the technological domain extend elsewhere. These observations shed doubt on the usefulness of the concept of cumulative culture, as defined presently. We have a relatively good understanding of technological change, which increases in complexity and efficiency over time, but is the same true about symbolic culture, norms and traditions? Can we reliably extrapolate our predictions to other domains? Does art count as cumulative culture? Does language? Moreover, comparative work has been interested in finding traces of cumulative culture in other species but, if we do, what does that tell us about cumulative culture and how does that change our understanding of human culture? Cumulative culture, in a narrow sense, has been a practical concept central to fruitful studies of the evolution of technology, but it is unclear whether using an extended sense of the concept would contribute beneficially to the study of human culture or if, conversely, would merely further ambiguity once we try to extend our understanding to other cultural domains.

6.4. Challenges and future work

If we are interested in how culture changes in a functional domain in which cultural traits have a clear utilitarian purpose, moving away from simple experimental design to include realistic large-scale tasks that can model cumulative culture in a naturalistic way is profoundly beneficial, as I have shown in this work. The dynamics of improvement over time can only be studied when individuals are allowed to freely explore an unbounded solution space, as was the case with the MATLAB contests we used here.

Although the MATLAB programming contest provided a realistic complex model of cumulative culture, its design still restricted the questions we could investigate. One obvious limitation relates to the fact that there was no objective way to identify which entries were copied by which, so I had to rely on similarity as an alternative method to measure cultural transmission. This allowed us to quantify the amount of novelty at the individual level, and the patterns of convergence at the population level, yet a more fine-grained measure of copying would have allowed us to track each solution back in time and answer different questions about solution relatedness, phylogenetic histories, and the amount of replication and blending in this type of cultural transmission. The experimental approach in Chapter 5 was also restricted by both the MATLAB framework and practical issues like recruiting and motivating participants. A higher sample size would have strengthened the results and increased empirical validity, but like with any experimental study there is a trade-off between more, better data and practical limitations. In our case, a higher sample size could have been ensured though more costly incentives, but would have also increased the cost of administrative effort.

Another clear limitation to this framework is the direct, obvious link between cultural artefacts and payoffs, which means our model of cumulative culture is applicable only to some types of culture. However, this paradigm could be easily extended to investigate the evolution of the kind of opaque culture that Henrich (2016) refers to, in which it is hard to judge both how a trait is constructed, and how beneficial it is, by manipulating the relationship between solutions and payoff. A simple way of doing this would be to remove payoff information completely from the contest and allow participants to purely judge solutions based on the code submitted. While this would encourage participants to inspect a more varied range of solutions and would potentially provide scope for increased innovation and recombination, we expect that the sheer number of solutions submitted would prevent a useful exploration of the search space. Other factors, like the identity of the submitter, could be used to judge the usefulness of a solution. For example, results showed a prestige effect emerging for individuals who achieved a leader status – this could then become a proxy for performance, and be used to guide social learning.

Adjusting visibility periods in the MATLAB contest would be a simple way of manipulating innovation rates and their effect on improvement. Most contests began with a ‘darkness’ period, where individuals could only see their own scores, thus working alone and developing their own solution, then followed by a full visibility ‘daylight’ period. Introducing a late ‘darkness’ period after ‘daylight’ would allow participants to discover and learn beneficial solutions from others, but also work alone on refining or modifying those solutions without the pressure of worrying that their solutions might be immediately copied. I anticipate this would allow for more exploration and potential innovation in solutions. The strong pressure for fast and cheap improvement seen in the contests is artificially strong, and I expect that reducing this pressure would lead to more naturalistic dynamics characterised by more cultural variation.

Similarly, manipulating group structure in this framework can answer questions regarding the dynamics of cultural diversity in a cumulative setting that result from splitting/merging events and migration. Chapter 5 implemented a simple group manipulation, but we can imagine a series of manipulations to systematically test how group size and splitting/merging events interact. Moving participants between groups throughout the contest can answer interesting questions regarding the role of migration in the diffusion of information. It could either be the case that participants conform to the local standards they migrate into, or it could be that an immigrant carrying a particularly useful solution can change the cultural make-up of the group it migrates into – I expect the answer to this question to be mediated by payoff pressures and payoff access.

Ultimately, this framework models how innovative, superior artefacts arise in a population mainly through many incremental improvements focused on improving the current leading solution, and rare remarkable novel solutions that could potentially introduce revolutionary innovations. Nonetheless, the convergence we see on solutions similar to the current best does not guarantee the population is necessarily converging on the best solutions - and, indeed, in this context an optimal solution is impossible in realistic time, which means the population is always entertaining imperfect solutions. These results speak to how collective improvements are achieved in a collaborative setting and can have direct practical implications for real world domains concerned with achieving progress. For example, science funding is presently concentrated on investing in the current leaders that have already proved successful, but this would suggest that improvement will be incremental, and the chances of revolutionary innovations decreased. Should it instead be pursuing diversity and innovation, accepting that this would increase the risk of failure? Experimental work focusing on the particular type of cumulative improvement studied here will provide meaningful insight into these questions.

For a more general understanding of cumulative culture, future work should attempt to focus on investigating how different learning and innovation processes involved affect the dynamics of cumulative improvement. We imagine learning in a cumulative setting represents a continuum between innovation and replication, with different processes like refinement, modification, and combination lying somewhere in between. The main process at work in the MATLAB contest was refinement, and I have briefly touched on recombination – this has also been the focus of recent experimental work (Derex and Boyd, 2016). More research focusing on these processes individually, and on examining the interactions between them, is needed in order to thoroughly understand the full range of learning strategies that have a role in cumulative culture.

Similarly, different tasks are expected to rely on different processes to different extents, so focusing on diverse, naturalistic cumulative tasks is essential for identifying what underlies human cultural change. Here I have shown that a programming competition can provide invaluable insight into these questions, and a large variety of similarly realistic datasets is not beyond reach. Studies have already explored how culture changes in the real world exploring the combinatorial nature of US patents (Youn *et al.*, 2015), the evolution and history of programming languages (Valverde and Solé, 2015), or using phylogenetic methods to reconstruct the history of tools (O'Brien, Darwent and Lyman, 2001) and musical instruments (Temkin and Eldredge, 2002), or even non-functional culture like fairy tales (Tehrani, 2013) and textiles (Tehrani and Collard, 2002). This gives us a good appreciation of how cultural traits change over time, so an obvious next step would be incorporating individual-level decisions to these realistic domains through experimental approaches for an inclusive understanding of cumulative cultural evolution.

6.5. Conclusion

The main task of the cultural evolution field is to explain cultural patterns by integrating simple individual-level decisions with population-level micro and macro-evolutionary patterns of cultural evolution, which interact in complex, non-straightforward ways. Experimental approaches can inform us with regards to individual-level processes, and complex theoretical modelling techniques and phylogenetic comparative methods can explain large-scale patterns of evolution over long periods of time. Therefore, a comprehensive view of the evolution of culture relies on linking individual and population-level dynamics and requires the use multiple complementary approaches. Ideally, theoretical observations will always be corroborated by real-world data, and this is what was attempted in this thesis by using theoretical and complex, naturalistic empirical methods to shed light on the drivers and dynamics of cumulative culture. I expect that, with time, this integration of methodological approaches will help crystallise our knowledge into a comprehensive understanding of human culture.

References

Acerbi, A., Kendal, J. and Tehrani, J. J. (2017) 'Cultural complexity and demography: the case of folktales', *Evolution and Human Behavior*, 38(4), pp. 474–480.

Acerbi, A. and Mesoudi, A. (2015) 'If we are all cultural Darwinians what's the fuss about? Clarifying recent disagreements in the field of cultural evolution', *Biology & Philosophy*, 30, pp. 481–503. doi: 10.1007/s10539-015-9490-2.

Acerbi, A., Tennie, C. and Mesoudi, A. (2016) 'Social learning solves the problem of narrow-peaked search landscapes : experimental evidence in humans', *Royal Society Open Science*, 3, p. 160215. doi: 10.1098/rsos.160215.

Allen, J., Weinrich, M., Hoppitt, W. and Rendell, L. (2013) 'Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales.', *Science*, 340, pp. 485–488. doi: 10.1126/science.1231976.

Andersson, C. and Törnberg, P. (2016) 'Fidelity and the speed of the treadmill: the combined impact of population size, transmission fidelity, and selection on the accumulation of cultural complexity', *American Antiquity*, 81(3), pp. 576–590. doi: 10.7183/0002-7316.81.3.576.

Aoki, K., Wakano, J. Y. and Lehmann, L. (2012) 'Evolutionarily stable learning schedules and cumulative culture in discrete generation models.', *Theoretical population biology*. Elsevier Inc., 81(4), pp. 300–9. doi: 10.1016/j.tpb.2012.01.006.

Apicella, C. L., Marlowe, F. W., Fowler, J. H. and Christakis, N. a (2012) 'Social networks and cooperation in hunter-gatherers.', *Nature*. Nature Publishing Group, 481(7382), pp. 497–501. doi: 10.1038/nature10736.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A. and Sheldon, B. C. (2014) 'Experimentally induced innovations lead to persistent culture via conformity in wild birds', *Nature*, 518(7540), pp. 538–541. doi:

10.1038/nature13998.

Asch, S. E. (1956) ‘Studies of independence and conformity: I. A minority of one against a unanimous majority.’, *Psychological Monographs: General and Applied*, 70(9), pp. 1–70. doi: 10.1037/h0093718.

Atkinson, Q. D., Meade, A., Venditti, C., Greenhill, S. J. and Pagel, M. (2008) ‘Languages evolve in punctuational bursts.’, *Science*, 319(5863), p. 588. doi: 10.1126/science.1149683.

Axelrod, R. and Hamilton, W. D. (1981) ‘The evolution of cooperation’, *Science*, 211(4489), pp. 1390–6.

Baldini, R. (2015) ‘Revisiting the effect of population size on cumulative cultural evolution’, *Journal of Cognition and Culture*, 15(3–4), pp. 320–336. doi: 10.1101/001529.

Basalla, G. (1988) *The evolution of technology*. Cambridge, UK: Cambridge University Press.

Bentley, R. A. and O’Brien, M. J. (2011) ‘The selectivity of social learning and the tempo of cultural evolution’, *Journal of Evolutionary Psychology*, 9(2), pp. 125–141. doi: 10.1556/JEP.9.2011.18.1.

van den Berg, P., Molleman, L. and Weissing, F. J. (2015) ‘Focus on the success of others leads to selfish behavior’, *Proceedings of the National Academy of Sciences*, p. 201417203. doi: 10.1073/pnas.1417203112.

Berl, R. E. W. and Hewlett, B. S. (2015) ‘Cultural variation in the use of overimitation by the Aka and Ngandu of the Congo Basin’, *PLoS ONE*, 10(3), p. e0120180. doi: 10.1371/journal.pone.0120180.

Bettencourt, L. M. a, Lobo, J., Helbing, D., Kühnert, C. and West, G. B. (2007) ‘Growth, innovation, scaling, and the pace of life in cities.’, *Proceedings of the National Academy of Sciences of the United States of America*, 104(17), pp. 7301–7306. doi: 10.1073/pnas.0610172104.

Boesch, C. (2003) ‘Is Culture a Golden Barrier Between Human and

Chimpanzee?', *Evolutionary Anthropology*, 12(2), pp. 82–91. doi: 10.1002/evan.10106.

Bond, R. and Smith, P. B. (1996) 'Culture and conformity: A meta-analysis of studies using Asch's (1952b, 1956) line judgment task.', *Psychological Bulletin*, 119(1), pp. 111–137. doi: 10.1037/0033-2909.119.1.111.

Borenstein, E., Feldman, M. W. and Aoki, K. (2008) 'Evolution of learning in fluctuating environments: when selection favors both social and exploratory individual learning.', *Evolution*, 62(3), pp. 586–602. doi: 10.1111/j.1558-5646.2007.00313.x.

Boyd, R. and Richerson, P. J. (1985) *Culture and the Evolutionary Process*. Chicago: University of Chicago Press. doi: 10.1097/00005053-198702000-00018.

Boyd, R. and Richerson, P. J. (1995) 'Why does culture increase human adaptability?', *Ethology and Sociobiology*, 16, pp. 125–143. doi: 10.1016/0162-3095(94)00073-G.

Boyd, R. and Richerson, P. J. (1996) 'Why culture is common, but cultural evolution is rare', *Proceeding of the British Academy*, 88, pp. 77–93.

Boyd, R. and Richerson, P. J. (2009) 'Culture and the evolution of human cooperation', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1533), pp. 3281–3288. doi: 10.1098/rstb.2009.0134.

Boyd, R., Richerson, P. J. and Henrich, J. (2011a) 'Rapid cultural adaptation can facilitate the evolution of large-scale cooperation.', *Behavioral Ecology and Sociobiology*, 65, pp. 431–444. doi: 10.1007/s00265-010-1100-3.

Boyd, R., Richerson, P. J. and Henrich, J. (2011b) 'The cultural niche: why social learning is essential for human adaptation.', *Proceedings of the National Academy of Sciences of the United States of America*, 108, pp. 10918–25. doi: 10.1073/pnas.1100290108.

Bray, J. R. and Curtis, J. T. (1957) 'An ordination of the upland forest communities of southern Wisconsin.', *Ecological Monographs*, 27(4), pp.

325–349.

Caldwell, C. A. and Millen, A. E. (2008) 'Experimental models for testing hypotheses about cumulative cultural evolution', *Evolution and Human Behavior*, 29(3), pp. 165–171. doi: 10.1016/j.evolhumbehav.2007.12.001.

Caldwell, C. A. and Millen, A. E. (2009) 'Social learning mechanisms and cumulative cultural evolution. Is imitation necessary?', *Psychological Science*, 20(12), pp. 1478–83. doi: 10.1111/j.1467-9280.2009.02469.x.

Caldwell, C. A. and Millen, A. E. (2010) 'Human cumulative culture in the laboratory: Effects of (micro) population size.', *Learning and Behavior*, 38(3), pp. 310–318. doi: 10.3758/LB.38.3.310.

Carlino, G. A., Chatterjee, S. and Hunt, R. M. (2007) 'Urban density and the rate of invention', *Journal of Urban Economics*, 61(3), pp. 389–419. doi: 10.1016/j.jue.2006.08.003.

Castro, L. and Toro, M. a (2014) 'Cumulative cultural evolution: the role of teaching.', *Journal of Theoretical Biology*, 347, pp. 74–83. doi: 10.1016/j.jtbi.2014.01.006.

Cavalli-Sforza, L. L. and Feldman, M. W. (1981) *Cultural transmission and evolution*. Princeton: Princeton University Press.

Centola, D. (2010) 'The spread of behavior in an online social network experiment.', *Science*, 329(5996), pp. 1194–7. doi: 10.1126/science.1185231.

Chudek, M. and Henrich, J. (2011) 'Culture-gene coevolution, norm-psychology and the emergence of human prosociality.', *Trends in Cognitive Sciences*, 15(5), pp. 218–226. doi: 10.1016/j.tics.2011.03.003.

Claidière, N., Scott-Phillips, T. C. and Sperber, D. (2014) 'How Darwinian is cultural evolution?', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369, p. 20130368.

Claidiere, N., Smith, K., Kirby, S. and Fagot, J. (2014) 'Cultural evolution of systematically structured behaviour in a non-human primate', *Proceedings of* *the Royal Society B: Biological Sciences*, 281, p. 20141541. doi: 10.1098/rspb.2014.1541.

Clarke, E. and Heyes, C. (2017) 'The swashbuckling anthropologist: Henrich on The Secret of Our Success', *Biology & Philosophy*, 32, pp. 289–305. doi: 10.1007/s10539-016-9554-y.

Collard, M., Buchanan, B., O'Brien, M. J. and Scholnick, J. (2013) 'Risk , mobility or population size? Drivers of technological richness among contact-period western North American hunter – gatherers', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(368), p. 20120412.

Collard, M., Kemery, M. and Banks, S. (2005) 'Causes of toolkit variation among hunter-gatherers: a test of four competing hypotheses', *Canadian Journal of Archaeology*, 29, pp. 1–19.

Collard, M., Ruttle, A., Buchanan, B. and O'Brien, M. J. (2013) 'Population size and cultural evolution in nonindustrial food-producing societies', *PloS ONE*, 8(9), p. e72628. doi: 10.1371/journal.pone.0072628.

Dawkins, R. and Carlisle, T. R. (1976) 'Parental investment, mate desertion and a fallacy', *Nature*, 262, pp. 131–133.

Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B. and Laland, K. N. (2012) 'Identification of the social and cognitive processes underlying human cumulative culture.', *Science*, 335(6072), pp. 1114–1118. doi: 10.1126/science.1213969.

Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E. and Kendal, R. L. (2013) 'Human cumulative culture: A comparative perspective', *Biological reviews of the Cambridge Philosophical Society*, 89(2), pp. 284–301. doi: 10.1111/brv.12053.

Derex, M., Beugin, M.-P., Godelle, B. and Raymond, M. (2013) 'Experimental evidence for the influence of group size on cultural complexity', *Nature*, 503(7476), pp. 389–391. doi: 10.1038/nature12774.

Derex, M. and Boyd, R. (2015) ‘The foundations of the human cultural niche.’, *Nature communications*, 6(May). doi: 10.1038/ncomms9398.

Derex, M. and Boyd, R. (2016) ‘Partial connectivity increases cultural accumulation within groups’, *Proceedings of the National Academy of Sciences*, 113(11), pp. 2982–2987. doi: 10.1073/pnas.1518798113.

Derex, M., Feron, R., Godelle, B. and Raymond, M. (2015) ‘Social learning and the replication process : an experimental investigation’, *Proc. R. Soc. B*, 282(1808), p. 20150719.

Derex, M., Godelle, B. and Raymond, M. (2013) ‘Social learners require process information to outperform individual learners’, *Evolution*, 67(3), pp. 688–697. doi: 10.5061/dryad.5ck3n.

Dice, L. R. (1945) ‘Measures of the amount of ecologic association between species’, *Ecology*, 26(3), pp. 297–302.

Dunn, M., Greenhill, S. J., Levinson, S. C. and Gray, R. D. (2011) ‘Evolved structure of language shows lineage-specific trends in word-order universals.’, *Nature*, 473(7345), pp. 79–82. doi: 10.1038/nature09923.

Efferson, C. M., Lalive, R., Richerson, P. J., McElreath, R. and Lubell, M. (2008) ‘Conformists and mavericks: the empirics of frequency-dependent cultural transmission’, *Evolution and Human Behavior*, 29(1), pp. 56–64. doi: 10.1016/j.evolhumbehav.2007.08.003.

Ehn, M. and Laland, K. (2012) ‘Adaptive strategies for cumulative cultural learning.’, *Journal of Theoretical Biology*, 301, pp. 103–11. doi: 10.1016/j.jtbi.2012.02.004.

Enquist, M. and Eriksson, K. (2007) ‘Critical points in current theory of conformist social learning’, *American Anthropologist*, 109(4), pp. 727–734. doi: 10.1525/AA.2007.109.4.727.728.

Enquist, M. and Ghirlanda, S. (2007) ‘Evolution of social learning does not explain the origin of human cumulative culture’, *Journal of Theoretical Biology*, 246(1), pp. 129–135. doi: 10.1016/j.jtbi.2006.12.022.

Enquist, M., Ghirlanda, S. and Eriksson, K. (2011) ‘Modelling the evolution and diversity of cumulative culture.’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1563), pp. 412–423. doi: 10.1098/rstb.2010.0132.

Enquist, M., Ghirlanda, S., Jarrick, A. and Wachtmeister, C.-A. (2008) ‘Why does human culture increase exponentially?’, *Theoretical Population Biology*, 74, pp. 46–55. doi: 10.1016/j.tpb.2008.04.007.

Enquist, M., Strimling, P., Eriksson, K., Laland, K. N. and Sjostrand, J. (2010) ‘One cultural parent makes no culture’, *Animal Behaviour*, 79(6), pp. 1353–1362. doi: 10.1016/j.anbehav.2010.03.009.

Eriksson, K. and Coultas, J. C. (2009) ‘Are people really conformist-biased? An empirical test and a new mathematical model’, *Journal of Evolutionary Psychology*, 7(1), pp. 5–21. doi: 10.1556/JEP.7.2009.1.3.

Eriksson, K., Enquist, M. and Ghirlanda, S. (2007) ‘Critical points in current theory of conformist social learning’, *Journal of Evolutionary Psychology*, 5(1), pp. 67–87. doi: 10.1556/JEP.2007.1009.

Fehér, O., Ljubičić, I., Suzuki, K., Okanoya, K. and Tchernichovski, O. (2017) ‘Statistical learning in songbirds: from self-tutoring to song culture’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1711), p. 20160053. doi: 10.1098/rstb.2016.0053.

Feldman, M., Aoki, K. and Kumm, J. (1996) ‘Individual versus social learning: Evolutionary analysis in a fluctuating environment’, *Anthropological Science*, 104(3), pp. 209–232.

Ferrari, S. L. P. and Cribari-Neto, F. (2004) ‘Beta begression for modelling rates and proportions’, *Journal of Applied Statistics*, 31(7), pp. 799–815. doi: 10.1080/0266476042000214501.

Fisher, J. and Hinde, R. A. (1949) ‘The opening of milk bottles by birds’, *British Birds*, 42(11), pp. 347–357.

Flynn, E. (2008) ‘Investigating children as cultural magnets: do young children transmit redundant information along diffusion chains?', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1509), pp. 3541–51. doi: 10.1098/rstb.2008.0136.

Flynn, E. and Smith, K. (2012) 'Investigating the Mechanisms of Cultural Acquisition', *Social Psychology*, 43(4), pp. 185–195. doi: 10.1027/1864-9335/a000119.

Fogarty, L., Strimling, P. and Laland, K. N. (2011) 'The evolution of teaching', *Evolution*, 65(10), pp. 2760–70. doi: 10.1111/j.1558-5646.2011.01370.x.

Fogarty, L., Wakano, J. Y., Feldman, M. W. and Aoki, K. (2017) 'The driving forces of cultural complexity', *Human Nature*, 28(1), pp. 39–52. doi: 10.1007/s12110-016-9275-6.

Fragaszy, D. and Perry, S. (2003) *The biology of animal traditions*. Cambridge: Cambridge University Press.

Franz, M. and Matthews, L. J. (2010) 'Social enhancement can create adaptive, arbitrary and maladaptive cultural traditions', *Proc. R. Soc. B*, 277(1698), pp. 3363–3372. doi: 10.1098/rspb.2010.0705.

Galef, B. G. (1992) 'The question of animal culture.', *Human Nature*, 3(2), pp. 157–78. doi: 10.1007/BF02692251.

Galef, B. G., Dudley, K. E. and Whiskin, E. E. (2008) 'Social learning of food preferences in "dissatisfied" and "uncertain" Norway rats', *Animal Behaviour*, 75(2), pp. 631–637. doi: 10.1016/j.anbehav.2007.06.024.

Giraldeau, L.-A. A., Valone, T. J. and Templeton, J. J. (2002) 'Potential disadvantages of using socially acquired information', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 357(1427), pp. 1559–66. doi: 10.1098/rstb.2002.1065.

Glowacki, L. and Molleman, L. (2017) 'Subsistence styles shape human social learning strategies', *Nature Human Behaviour*, 1, p. 98. doi: 10.1038/s41562-017-0098.

Gross, R., Houston, A. I., Collins, E. J., McNamara, J. M., Dechaume-Moncharmont, F.-X. and Franks, N. R. (2008) ‘Simple learning rules to cope with changing environments.’, *Journal of the Royal Society Interface*, 5(27), pp. 1193–202. doi: 10.1098/rsif.2007.1348.

Gruber, T., Muller, M. N., Reynolds, V., Wrangham, R. and Zuberbühler, K. (2011) ‘Community-specific evaluation of tool affordances in wild chimpanzees’, *Scientific Reports*, 1, p. 128. doi: 10.1038/srep00128.

Henrich, J. (2004) ‘Demography and cultural evolution: How adaptive cultural processes can produce maladaptive losses - the Tasmanian case’, *American Antiquity*, 69(2), pp. 197–214. doi: 10.2307/4128416.

Henrich, J. (2006) ‘Understanding cultural evolutionary models : A reply to read’s critique’, *American Antiquity*, 71(4), pp. 771–782. doi: 10.2307/40035890.

Henrich, J. (2016) *The secret of our success: how culture is driving human evolution, domesticating our species, and making us smarter*. Princeton: Princeton University Press.

Henrich, J. and Boyd, R. (1998) ‘The evolution of conformist transmission and the emergence of between-group differences’, *Evolution and Human Behavior*, 19(4), pp. 215–241. doi: 10.1016/S1090-5138(98)00018-X.

Henrich, J. and Broesch, J. (2011) ‘On the nature of cultural transmission networks: evidence from Fijian villages for adaptive learning biases’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), pp. 1139–1148. doi: 366/1567/1139 [pii]\r10.1098/rstb.2010.0323.

Henrich, J. and Gil-White, F. J. (2001) ‘The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission’, *Evolution and Human Behavior*, 22(3), pp. 165–196. doi: 10.1016/S1090-5138(00)00071-4.

Henrich, J., Heine, S. J. and Norenzayan, A. (2010) ‘The weirdest people in the world?’, *Behavioral and Brain Sciences*, 33, pp. 61–135. doi:

10.1017/S0140525X0999152X.

Henrich, J. and Henrich, N. (2010) ‘The evolution of cultural adaptations : Fijian food taboos protect against dangerous marine toxins’, *Proceedings of the Royal Society B: Biological Sciences*, 277, pp. 3715–3724. doi: 10.1098/rspb.2010.1191.

Henrich, J. and McElreath, R. (2003) ‘The evolution of cultural evolution’, *Evolutionary Anthropology: Issues, News, and Reviews*, 12(3), pp. 123–135. doi: 10.1002/evan.10110.

Hewlett, B. S. L., Fouts, H. N., Boyette, A. H. and Hewlett, B. S. L. (2011) ‘Social learning among Congo Basin hunter-gatherers’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), pp. 1168–1178. doi: 10.1098/rstb.2010.0373.

Heyes, C. (2012a) ‘Grist and mills: on the cultural origins of cultural learning.’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1599), pp. 2181–91. doi: 10.1098/rstb.2012.0120.

Heyes, C. (2012b) ‘What’s social about social learning?’, *Journal of Comparative Psychology*, 126(2), pp. 193–202. doi: 10.1037/a0025180.

Heyes, C. M. (1994) ‘Social learning in animals: categories and mechanisms.’, *Biological Reviews*, 69(2), pp. 207–31.

Heyes, C. and Pearce, J. M. (2015) ‘Not-so-social learning strategies’, *Proceedings of the Royal Society B: Biological Sciences*, 282, p. 20141709.

Hill, K. R., Wood, B. M., Baggio, J., Hurtado, a M. and Boyd, R. T. (2014) ‘Hunter-Gatherer Inter-Band Interaction Rates: Implications for Cumulative Culture.’, *PLoS ONE*, 9(7), p. e102806. doi: 10.1371/journal.pone.0102806.

Hinde, R. A. and Fisher, J. (1951) ‘Further observations on the opening of milk bottles by birds’, *British Birds*, 44(12), pp. 393–396. doi: 10.1038/1691006a0.

Hoppitt, W. and Laland, K. N. (2013) *Social learning: An introduction to mechanisms, methods, and models*. Princeton University Press.

Horner, V. and Whiten, A. (2005) ‘Causal knowledge and imitation/emulation switching in chimpanzees (Pan troglodytes) and children (Homo sapiens).’, *Animal cognition*, 8(3), pp. 164–81. doi: 10.1007/s10071-004-0239-6.

Horner, V., Whiten, A., Flynn, E. and de Waal, F. B. M. (2006) ‘Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children.’, *Proceedings of the National Academy of Sciences of the United States of America*, 103(37), pp. 13878–83. doi: 10.1073/pnas.0606015103.

Hrubesch, C., Preuschoft, S. and van Schaik, C. (2009) ‘Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (Pan troglodytes).’, *Animal cognition*, 12(2), pp. 209–16. doi: 10.1007/s10071-008-0183-y.

Hunt, G. R. and Gray, R. D. (2003) ‘Diversification and cumulative evolution in New Caledonian crow tool manufacture.’, *Proceedings. Biological sciences / The Royal Society*, 270(1517), pp. 867–74. doi: 10.1098/rspb.2002.2302.

Jordan, F. M., Gray, R. D., Greenhill, S. J. and Mace, R. (2009) ‘Matrilocal residence is ancestral in Austronesian societies’, *Proceedings of the Royal Society B: Biological Sciences*, 276, pp. 1957–64. doi: 10.1098/rspb.2009.0088.

Kameda, T. and Nakanishi, D. (2002) ‘Cost – benefit analysis of social / cultural learning in a nonstationary uncertain environment An evolutionary simulation and an experiment with human subjects’, *Evolution and Human Behavior*, 23, pp. 373–393.

Kameda, T. and Nakanishi, D. (2003) ‘Does social/cultural learning increase human adaptability? Rogers’s question revisited’, *Evolution and Human Behavior*, 24(4), pp. 242–260. doi: 10.1016/S1090-5138(03)00015-1.

Kandler, A. and Steele, J. (2009) ‘Social learning, economic inequality, and innovation diffusion’, in O’Brien, M. J. and Shennan, S. J. (eds) *Innovation in cultural systems*. Cambridge MA: The MIT Press, pp. 193–214.

Karp, R. M. (2010) ‘Reducibility among combinatorial problems’, in *50 Years of Integer Programming 1958-2008: From the Early Years to the State-of-the-Art*, pp. 219–241. doi: 10.1007/978-3-540-68279-0_8.

Kawai, M. (1965) ‘Newly acquired pre-cultural behaviour of the natural troop of Japanese monkeys on Koshima inlet’, *Primates*, 6(1), pp. 1–30. doi: 10.1007/BF01794457.

Kawamura, S. (1959) ‘The process of sub-culture propagation among Japanese macaques’, *Primates*, 2(1), pp. 43–60.

Kempe, M., Lycett, S. J. and Mesoudi, A. (2014) ‘From cultural traditions to cumulative culture: Parameterizing the differences between human and nonhuman culture’, *Journal of Theoretical Biology*. Elsevier, 359, pp. 29–36. doi: 10.1016/j.jtbi.2014.05.046.

Kempe, M. and Mesoudi, A. (2014) ‘An experimental demonstration of the effect of group size on cultural accumulation’, *Evolution and Human Behavior*. Elsevier B.V., 35(4), pp. 285–290. doi: 10.1016/j.evolhumbehav.2014.02.009.

Kendal, J., Giraldeau, L.-A. and Laland, K. (2009) ‘The evolution of social learning rules: payoff-biased and frequency-dependent biased transmission.’, *Journal of theoretical biology*, 260(2), pp. 210–9. doi: 10.1016/j.jtbi.2009.05.029.

Kendal, R. L., Coolen, I., van Bergen, Y. and Laland, K. N. (2005) ‘Trade-offs in the adaptive use of social and asocial learning’, *Advances in the Study of Behavior*, 35, pp. 333–379. doi: 10.1016/S0065-3454(05)35008-X.

Kirby, S., Cornish, H. and Smith, K. (2008) ‘Cumulative cultural evolution in the laboratory: an experimental approach to the origins of structure in human language.’, *Proceedings of the National Academy of Sciences of the United States of America*, 105(31), pp. 10681–6. doi: 10.1073/pnas.0707835105.

Kline, M. A. and Boyd, R. (2010) ‘Population size predicts technological complexity in Oceania.’, *Proceedings of the Royal Society B: Biological*

Sciences, 277(1693), pp. 2559–2564. doi: 10.1098/rspb.2010.0452.

Kobayashi, Y. and Aoki, K. (2012) ‘Innovativeness, population size and cumulative cultural evolution’, *Theoretical Population Biology*. Elsevier Inc., 82(1), pp. 38–47. doi: 10.1016/j.tpb.2012.04.001.

Kobayashi, Y., Ohtsuki, H. and Wakano, J. Y. (2016) ‘Population size vs. social connectedness — A gene-culture coevolutionary approach to cumulative cultural evolution’, *Theoretical Population Biology*. doi: 10.1016/j.tpb.2016.07.001.

Kurzban, R. and Barrett, H. C. (2012) ‘Origins of Cumulative Culture’, *Science*, 335(2012), pp. 1056–1057. doi: 10.1126/science.1219232.

Kushnick, G., Gray, R. D. and Jordan, F. M. (2014) ‘The sequential evolution of land tenure norms’, *Evolution and Human Behavior*, 35(4), pp. 309–318. doi: 10.1016/j.evolhumbehav.2014.03.001.

Laland, K. N. (2004) ‘Social learning strategies.’, *Learning & Behavior*, 32(1), pp. 4–14.

Laland, K. N. (2017) *Darwin’s Unfinished Symphony: How Culture Made the Human Mind*. Princeton University Press.

Laland, K. N., Odling-Smee, J. and Feldman, M. W. (2000) ‘Niche construction, biological evolution, and cultural change’, *Behavioral and Brain Sciences*, 23(1), pp. 131–146. doi: 10.1017/S0140525X00002417.

Lane, D. A. (2016) ‘Innovation cascades : artefacts , organization and attributions’, *Philosophical transactions of the Royal Society. Series B: Biological Sciences*, 371(1690), p. 20150194. doi: 10.1098/rstb.2015.0194.

van Leeuwen, E. J. C. and Haun, D. B. M. (2014) ‘Conformity without majority? The case for demarcating social from majority influences’, *Animal Behaviour*, 96, pp. 187–194. doi: 10.1016/j.anbehav.2014.08.004.

Legare, C. H. (2017) ‘Cumulative cultural learning: Development and Diversity’, *in press*.

Lehmann, L., Aoki, K. and Feldman, M. W. (2011) ‘On the number of independent cultural traits carried by individuals and populations.’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1563), pp. 424–35. doi: 10.1098/rstb.2010.0313.

Lewis, H. M. and Laland, K. N. (2012) ‘Transmission fidelity is the key to the build-up of cumulative culture.’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1599), pp. 2171–2180. doi: 10.1098/rstb.2012.0119.

Lupyan, G. and Dale, R. (2010) ‘Language structure is partly determined by social structure’, *PLoS ONE*, 5(1). doi: 10.1371/journal.pone.0008559.

Lyons, D. E., Damrosch, D. H., Lin, J. K., Macris, D. M. and Keil, F. C. (2011) ‘The scope and limits of overimitation in the transmission of artefact culture.’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), pp. 1158–67. doi: 10.1098/rstb.2010.0335.

Lyons, D. E., Young, A. G. and Keil, F. C. (2007) ‘The hidden structure of overimitation.’, *Proceedings of the National Academy of Sciences of the United States of America*, 104(50), pp. 19751–6. doi: 10.1073/pnas.0704452104.

Marshall-Pescini, S. and Whiten, A. (2008) ‘Chimpanzees (Pan troglodytes) and the question of cumulative culture: an experimental approach.’, *Animal Cognition*, 11(3), pp. 449–56. doi: 10.1007/s10071-007-0135-y.

Mathew, S. and Perreault, C. (2015) ‘Behavioural variation in 172 small-scale societies indicates that social learning is the main mode of human adaptation’, *Proceedings of the Royal Society B: Biological Sciences*, 282(1810), p. 20150061. doi: 10.1098/rspb.2015.0061.

McCabe, T. J. (1976) ‘A complexity measure’, *IEEE Transactions on Software Engineering*, 2(4), pp. 308–320.

McElreath, R., Bell, A. V, Efferson, C., Lubell, M., Richerson, P. J. and Waring, T. (2008) ‘Beyond existence and aiming outside the laboratory: estimating frequency-dependent and pay-off-biased social learning strategies.', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1509), pp. 3515–28. doi: 10.1098/rstb.2008.0131.

McElreath, R., Lubell, M., Richerson, P. J., Waring, T. M., Baum, W., Edsten, E., Efferson, C. and Paciotti, B. (2005) 'Applying evolutionary models to the laboratory study of social learning', *Evolution and Human Behavior*, 26(6), pp. 483–508. doi: 10.1016/j.evolhumbehav.2005.04.003.

Mesoudi, A. (2008) 'An experimental simulation of the "copy-successful-individuals" cultural learning strategy: adaptive landscapes, producer – scrounger dynamics, and informational access costs', *Evolution and Human Behavior*, 29, pp. 350–363. doi: 10.1016/j.evolhumbehav.2008.04.005.

Mesoudi, A. (2011a) 'An experimental comparison of human social learning strategies: payoff-biased social learning is adaptive but underused', *Evolution and Human Behavior*, 32(5), pp. 334–342. doi: 10.1016/j.evolhumbehav.2010.12.001.

Mesoudi, A. (2011b) *Cultural evolution: How Darwinian theory can explain human culture and synthesize the social sciences*. University of Chicago Press.

Mesoudi, A. (2011c) 'Variable Cultural Acquisition Costs Constrain Cumulative Cultural Evolution', *PLoS ONE*, 6(3), p. e18239. doi: 10.1371/journal.-pone.0018239.

Mesoudi, A. (2015) 'Cultural Evolution: A Review of Theory, Findings and Controversies', *Evolutionary Biology*. Springer US, 43(4), pp. 481–497. doi: 10.1007/s11692-015-9320-0.

Mesoudi, A., Chang, L., Dall, S. R. X. and Thornton, A. (2016) 'The evolution of individual and cultural variation in social learning', *Trends in Ecology and Evolution*, 31(3), pp. 215–225. doi: 10.1016/j.tree.2015.12.012.

Mesoudi, A., Chang, L., Murray, K. and Lu, H. J. (2015) 'Higher frequency of social learning in China than in the West shows cultural variation in the dynamics of cultural evolution', *Proceedings of the Royal Society B*, 282, p.

20142209. doi: 10.1098/rspb.2014.2209.

Mesoudi, A. and Whiten, A. (2008) ‘The multiple roles of cultural transmission experiments in understanding human cultural evolution’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1509), pp. 3489–501. doi: 10.1098/rstb.2008.0129.

Mesoudi, A., Whiten, A. and Dunbar, R. (2006) ‘A bias for social information in human cultural transmission’, *British Journal of Psychology*, 97(3), pp. 405–423. doi: 10.1348/000712605X85871.

Molleman, L., van den Berg, P. and Weissing, F. J. (2014) ‘Consistent individual differences in human social learning strategies.’, *Nature Communications*, 5, p. 3570. doi: 10.1038/ncomms4570.

Morgan, T. J. H. and Laland, K. N. (2012) ‘The biological bases of conformity.’, *Frontiers in Neuroscience*, 6, p. 87. doi: 10.3389/fnins.2012.00087.

Morgan, T. J. H., Rendell, L. E., Ehn, M., Hoppitt, W. and Laland, K. N. (2012) ‘The evolutionary basis of human social learning’, *Proc. R. Soc. B*, 279(1729), pp. 653–662. doi: 10.1098/rspb.2011.1172.

Morgan, T. J. H., Uomini, N. T., Rendell, L. E., Chouinard-Thuly, L., Street, S. E., Lewis, H. M., Cross, C. P., Evans, C., Kearney, R., de la Torre, I., Whiten, A. and Laland, K. N. (2015) ‘Experimental evidence for the co-evolution of hominin tool-making teaching and language’, *Nature Communications*, 6, p. 6029. doi: 10.1038/ncomms7029.

Morin, O. (2015) *How traditions live and die*. Oxford University Press.

Morin, O. (2016) ‘Reasons to be fussy about cultural evolution’, *Biology and Philosophy*. Springer Netherlands, 31(3), pp. 447–458. doi: 10.1007/s10539-016-9516-4.

Muthukrishna, M. and Henrich, J. (2016) ‘Innovation in the collective brain’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371, p. 20150192. doi: 10.1098/rstb.2015.0192.

Muthukrishna, M., Shulman, B. W., Vasilescu, V. and Henrich, J. (2013) 'Sociality influences cultural complexity', *Proceedings of the Royal Society B: Biological Sciences*, 281(1774), pp. 2013–2511.

Nakahashi, W. (2007) 'The evolution of conformist transmission in social learning when the environment changes periodically', *Theoretical Population Biology*, 72(1), pp. 52–66. doi: 10.1016/j.tpb.2007.03.003.

Nakahashi, W. (2014) 'The effect of cultural interaction on cumulative cultural evolution', *Journal of Theoretical Biology*, 352, pp. 6–15. doi: 10.1016/j.jtbi.2014.02.032.

Nettle, D. (2012) 'Social scale and structural complexity in human languages', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1597), pp. 1829–1836. doi: 10.1098/rstb.2011.0216.

O'Brien, M. J., Boulanger, M. T., Buchanan, B., Collard, M., Lee Lyman, R. and Darwent, J. (2014) 'Innovation and cultural transmission in the American Paleolithic: Phylogenetic analysis of eastern Paleoindian projectile-point classes', *Journal of Anthropological Archaeology*, 34(1), pp. 100–119. doi: 10.1016/j.jaa.2014.03.001.

O'Brien, M. J., Darwent, J. and Lyman, R. L. (2001) 'Cladistics is useful for reconstructing archaeological phylogenies : Palaeoindian points from the Southeastern United', *Journal of Archaeological Science*, 28, pp. 1115–1136. doi: 10.1006/jasc.2001.0681.

Oswalt, W. H. (1976) *An anthropological analysis of food-getting technology*. New York: John Wiley.

Pagel, M. (2009) 'Human language as a culturally transmitted replicator.', *Nature reviews. Genetics*, 10(6), pp. 405–415. doi: 10.1038/nrg2560.

Perry, S., Baker, M., Fedigan, L., Gros-louis, J., Jack, K., Mackinnon, K. C., Manson, J. H., Panger, M., Pyle, K. and Rose, L. (2003) 'Social conventions in wild white-faced capuchin monkeys', *Current Anthropology*, 44(2), pp. 241–269.

Pike, T. W. and Laland, K. N. (2010) ‘Conformist learning in nine-spined sticklebacks’ foraging decisions.’, *Biology Letters*, 6(4), pp. 466–468. doi: 10.1098/rsbl.2009.1014.

Plummer, M. (2003) ‘JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling’, *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*, pp. 20–22. doi: 10.1.1.13.3406.

Powell, A., Shennan, S. and Thomas, M. G. (2009) ‘Late Pleistocene demography and the appearance of modern human behavior’, *Science*, 324(5932), pp. 1298–301. doi: 10.1126/science.1170165.

Pradhan, G. R., Tennie, C. and van Schaik, C. P. (2012) ‘Social organization and the evolution of cumulative technology in apes and hominins.’, *Journal of Human Evolution*. Elsevier Ltd, 63, pp. 180–190. doi: 10.1016/j.jhevol.2012.04.008.

Read, D. (2006) ‘Tasmanian knowledge and skill : maladaptive imitation or adequate technology?’, *American Antinquity*, 71(1), pp. 164–184.

Read, D. D. (2009) ‘The misuse of a mathematical model: the Tasmanian case (Reply to Henrich’s Response)’, *Human Complex Systems*.

Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M. W., Fogarty, L., Ghirlanda, S., Lillicrap, T. and Laland, K. N. (2010) ‘Why copy others? Insights from the social learning strategies tournament’, *Science*, 328(5975), pp. 208–213.

Rendell, L., Boyd, R., Enquist, M., Feldman, M. W., Fogarty, L. and Laland, K. N. (2011) ‘How copying affects the amount, evenness and persistence of cultural knowledge: insights from the social learning strategies tournament’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), pp. 1118–1128. doi: 10.1098/rstb.2010.0376.

Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. J. H., Webster, M. M. and Laland, K. N. (2011) ‘Cognitive culture: theoretical and empirical insights into social learning strategies', *Trends in Cognitive Sciences*, 15(2), pp. 68–76. doi: 10.1016/j.tics.2010.12.002.

Rendell, L., Fogarty, L. and Laland, K. N. (2010) 'Rogers' paradox recast and resolved: population structure and the evolution of social learning strategies.', *Evolution*, 64(2), pp. 534–548. doi: 10.1111/j.1558-5646.2009.00817.x.

Rendell, L. and Whitehead, H. (2001) 'Culture in whales and dolphins.', *The Behavioral and brain sciences*, 24(2), pp. 309-24-82.

Richerson, P. J. and Boyd, R. (2005) *Not by Genes Alone: How Culture Transformed Human Evolution*. Chicago: University of Chicago Press. doi: 10.1111/j.1467-9744.2009.01005.x.

Rieucau, G. and Giraldeau, L.-A. (2011) 'Exploring the costs and benefits of social information use: an appraisal of current experimental evidence', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), pp. 949–957. doi: 10.1098/rstb.2010.0325.

Roche, D. G., Careau, V. and Binning, S. A. (2016) 'Demystifying animal "personality" (or not): why individual variation matters to experimental biologists', *The Journal of Experimental Biology*, 219(24), pp. 3832–3843. doi: 10.1242/jeb.146712.

Rogers, A. R. (1988) 'Does biology constrain culture ?', *American Anthropologist*, 90(4), pp. 819–831.

Sasaki, T. and Biro, D. (2017) 'Cumulative culture can emerge from collective intelligence in animal groups', *Nature Communications*, 8, p. 15049. doi: 10.1038/ncomms15049.

van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S. and Merrill, M. (2003) 'Orangutan cultures and the evolution of material culture', *Science*, 299(5603), pp. 102–105.

Schlag, K. H. (1998) 'Why Imitate, and If So, How?', *Journal of Economic Theory*, 78(1), pp. 130–156. doi: 10.1006/jeth.1997.2347.

Shennan, S. (2001) ‘Demography and cultural innovation: a model and its implications for the emergence of modern human culture’, *Cambridge Archaeological Journal*, 11(1), pp. 5–16. doi: 10.1017/S0959774301000014.

Shennan, S. (2011) ‘Descent with modification and the archaeological record Descent with modification and the archaeological record’, *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 366, pp. 1070–1079. doi: 10.1098/rstb.2010.0380.

Sih, A., Bell, A. and Johnson, J. C. (2004) ‘Behavioral syndromes: An ecological and evolutionary overview’, *Trends in Ecology and Evolution*, pp. 372–378. doi: 10.1016/j.tree.2004.04.009.

Smith, B. and Wilson, J. B. (1996) ‘A consumer’s guide to evenness indices’, *Oikos*, 76(1), pp. 70–82.

Sørensen, T. (1948) ‘A method of establishing groups of equal amplitude in plant sociology based on similarity of species content’, *Kongelige Danske Videnskabernes Selskab*, 5, pp. 4–7.

Sterelny, K. (2011) ‘From hominins to humans : how sapiens became behaviourally modern’, pp. 809–822. doi: 10.1098/rstb.2010.0301.

Sterelny, K. (2017) ‘Cultural evolution in California and Paris’, *Studies in History and Philosophy of Biological and Biomedical Sciences*, 62, pp. 42–50. doi: 10.1016/j.shpsc.2016.12.005.

Strimling, P., Sjöstrand, J., Enquist, M. and Eriksson, K. (2009) ‘Accumulation of independent cultural traits’, *Theoretical Population Biology*. Elsevier Inc., 76(2), pp. 77–83. doi: 10.1016/j.tpb.2009.04.006.

Stubbersfield, J. M., Tehrani, J. J. and Flynn, E. G. (2015) ‘Serial killers, spiders and cybersex: Social and survival information bias in the transmission of urban legends’, *British Journal of Psychology*, 106(2), pp. 288–307. doi: 10.1111/bjop.12073.

Stubbersfield, J. M., Tehrani, J. J. and Flynn, E. G. (2017) ‘Chicken tumours and a fishy revenge: evidence for emotional content bias in the cultural transmission of urban legends', *Journal of Cognition and Culture*, 17(1–2), pp. 12–26.

Team, R. C. (2016) 'R: A language and environment for statistical computing'. Vienna, Austria: Foundation for Statistical Computing.

Tehrani, J. and Collard, M. (2002) 'Investigating cultural evolution through biological phylogenetic analyses of Turkmen textiles', *Journal of Anthropological Archaeology*, pp. 443–463. doi: 10.1016/S0278-4165(02)00002-8.

Tehrani, J. J. (2013) 'The phylogeny of Little Red Riding Hood', *PLoS ONE*, 8(11), p. e78871. doi: 10.1371/journal.pone.0078871.

Temkin, I. and Eldredge, N. (2002) 'Phylogenetics and material cultural evolution', *Curr. Anthropol.*, 28, pp. 146–153.

Tennie, C., Call, J. and Tomasello, M. (2009) 'Ratcheting up the ratchet: on the evolution of cumulative culture.', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1528), pp. 2405–15. doi: 10.1098/rstb.2009.0052.

Terkel, J. (1995) 'Cultural Transmission in the Black Rat: Pine Cone Feeding', *Advance*, 24, pp. 119–154. doi: 10.1016/S0065-3454(08)60393-9.

Thornton, A. and Lukas, D. (2012) 'Individual variation in cognitive performance: developmental and evolutionary perspectives', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1603), pp. 2773–2783. doi: 10.1098/rstb.2012.0214.

Thornton, A. and Mcauliffe, K. (2014) 'Teaching in Wild Meerkats', 227(2006). doi: 10.1126/science.1128727.

Toelch, U., Bruce, M. J., Meeus, M. T. H. and Reader, S. M. (2011) 'Social performance cues induce behavioral flexibility in humans', *Frontiers in Psychology*, 2, p. 160. doi: 10.3389/fpsyg.2011.00160.

Toelch, U., Bruce, M. J., Newson, L., Richerson, P. J. and Reader, S. M. (2013)

‘Individual consistency and flexibility in human social information use’, *Proceedings of the Royal Society B: Biological Sciences*, 281, p. 20132864. doi: 10.1098/rspb.2013.2864.

Tomasello, M. (1996) ‘Ch. 15 Do apes ape?’, in *Social Learning in Animals*, pp. 319–346. doi: 10.1016/B978-012273965-1/50016-9.

Tomasello, M. (1999) *The Cultural Origins of Human Cognition*. Harvard University Press.

Tomasello, M., Kruger, A. C. and Ratner, H. H. (1993) ‘Cultural learning’, *Behavioral and Brain Sciences*, 16(3), pp. 495–552. doi: 10.1017/S0140525X00031496.

Vaesen, K. (2012) ‘Cumulative cultural evolution and demography’, *PLoS ONE*, 7(7), p. e40989. doi: 10.1371/journal.pone.0040989.

Valverde, S. and Solé, R. V (2015) ‘Punctuated equilibrium in the large-scale evolution of programming languages’, *Journal of the Royal Society, Interface*, 12, p. 20150249. doi: 10.1098/rsif.2015.0249.

van de Waal, E., Borgeaud, C. and Whiten, A. (2013) ‘Potent social learning and conformity shape a wild primate’s foraging decisions’, *Science*, 340(6131), pp. 483–485.

van de Waal, E., Claidière, N. and Whiten, A. (2013) ‘Social learning and spread of alternative means of opening an artificial fruit in four groups of vervet monkeys’, *Animal Behaviour*, 85(1). doi: 10.1016/j.anbehav.2012.10.008.

Wang, J., Veugelers, R. and Stephan, P. (2016) ‘Bias against novelty in science: a cautionary tale for users of bibliometric indicators’, *NBER Working Paper Series*, (No. w22180). doi: 10.3386/w22180.

Wasielewski, H. (2014) ‘Imitation Is necessary for cumulative cultural evolution in an unfamiliar, ppaque task’, *Human Nature*, 25(1), pp. 161–179. doi: 10.1007/s12110-014-9192-5.

Webster, M. M. and Laland, K. N. (2011) ‘Reproductive state affects reliance on public information in sticklebacks’, *Proceedings of the Royal Society B: Biological Sciences*, 278(1705), pp. 619–627. doi: 10.1098/rspb.2010.1562.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. and Boesch, C. (1999) ‘Cultures in chimpanzees’, *Nature*, 399(6737), pp. 682–685. doi: 10.1038/21415.

Whiten, A., Spiteri, A., Horner, V., Bonnie, K. E., Lambeth, S. P., Schapiro, S. J. and de Waal, F. B. M. (2007) ‘Transmission of multiple traditions within and between chimpanzee groups.’, *Current Biology*, 17, pp. 1038–43. doi: 10.1016/j.cub.2007.05.031.

Xu, J., Dowman, M. and Griffiths, T. L. (2013) ‘Cultural transmission results in convergence towards colour term universals’, *Proceedings of the Royal Society B: Biological Sciences*, 280, p. 20123073.

Yamamoto, S., Humle, T. and Tanaka, M. (2013) ‘Basis for Cumulative Cultural Evolution in Chimpanzees: Social Learning of a More Efficient Tool-Use Technique’, *PLoS ONE*, 8(1). doi: 10.1371/journal.pone.0055768.

Youn, H., Strumsky, D., Bettencourt, L. M. A. and Lobo, J. (2015) ‘Invention as a combinatorial process: evidence from US patents.’, *Journal of the Royal Society, Interface / the Royal Society*, 12(106), p. 20150272-. doi: 10.1098/rsif.2015.0272.

Appendix

Supplementary figures

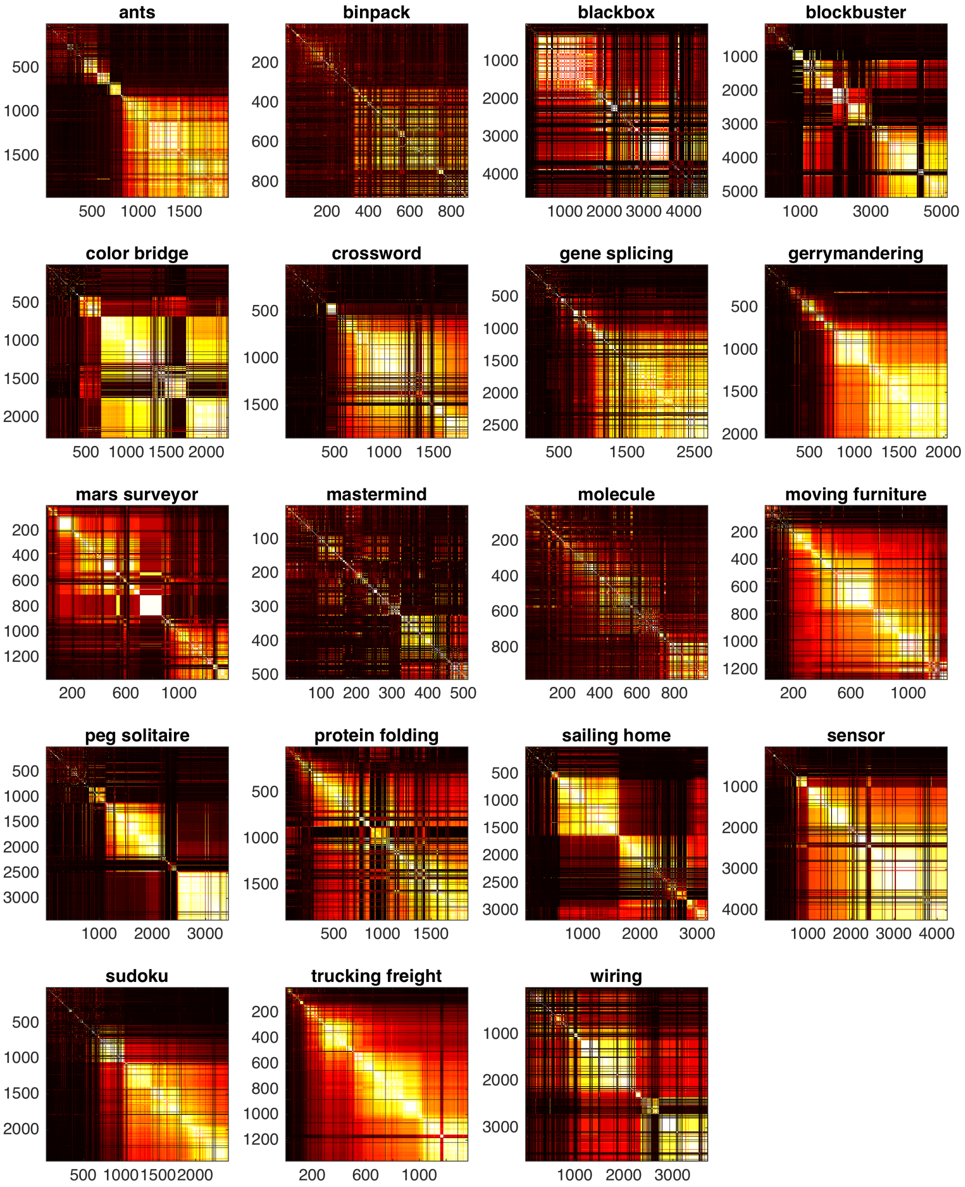


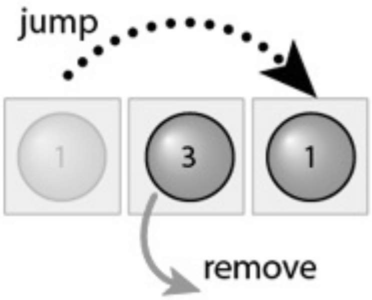
Figure A1 – Code similarity matrices between all pairs of passed entries in all 19 contests.

Contest description example

Peg Solitaire, May 2007

This contest is based on a simple peg jumping game. In a typical game of Peg Solitaire, the board contains pegs (sometimes marbles) and at least one empty space. Pegs can be removed by jumping over them with another peg, and the aim is to remove as many pegs with a combination of jumping moves.

This implements an extended version of the original Peg Solitaire game, in which the pegs carry points, and the goal is to jump pegs in order to make the score as low as possible. This may mean it is not necessary to remove all the pegs. Each peg has a value, or weight. A move consists of one peg jumping over and thereby removing another peg. A "jump" is a horizontal or vertical move in which one peg passes over exactly one other peg and comes to rest on an empty space. Diagonal jumps are not permitted. There is a reward for every peg removed from the board according to its weight, and a penalty for each jump according to the weight of the jumping peg. The score is therefore the difference between the value of the peg being jumped over and the jumping peg. Therefore a good score can be achieved by jumping with a low value peg over a high value peg; the bigger the difference between the values of the two pegs, the better the score. If, however, a high value peg is used to jump over a low value peg, the score decreases.



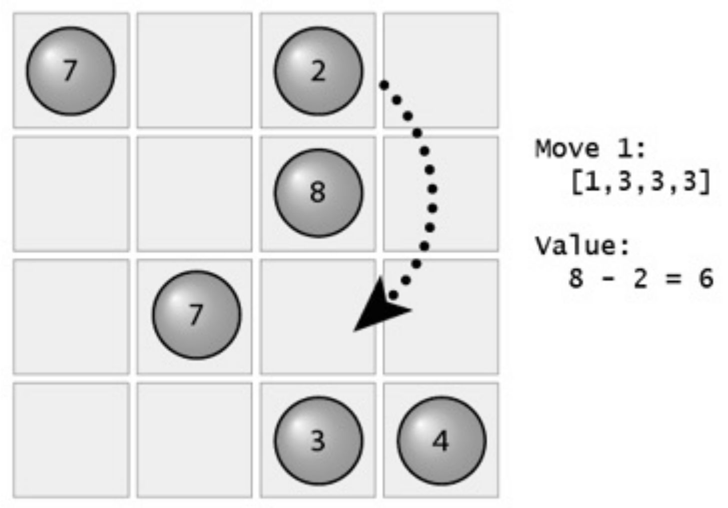
A peg with weight 1 jumps over a peg with weight 3. The reward is 3 and the penalty is 1, therefore the value of the move is 2. If several jumps in a row can be performed using the same peg, the penalty only has to be paid once.

In more detail:

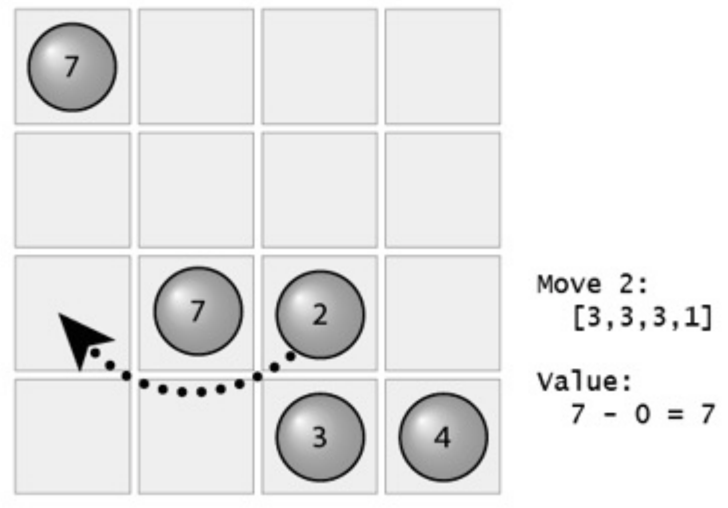
- Each peg has a weight, which is always positive.
- The board is a matrix. Each positive number indicates a peg, zeros indicate empty squares, and negative numbers indicate off limits squares outside of the board.
- Every move is a four-element row vector with the format [from_row from_column to_row to_column]

- The code must return a four-column move matrix in which each row represents one move. This matrix can have any number of rows between 0 and (numpegs – 1). Any number of rows exceeding this is ignored.
- The value of each move is the sum of the removal bonus and the jumping penalty.
- Consecutive moves by a single peg only incur one jumping penalty.
- The score starts at a high value (the sum of all the peg weights). After each move, the point value of that move is subtracted from the score. The foal is to minimize the score
- An invalid move does not generate an error – the board remains unchanged and the jumping penalty is still paid.

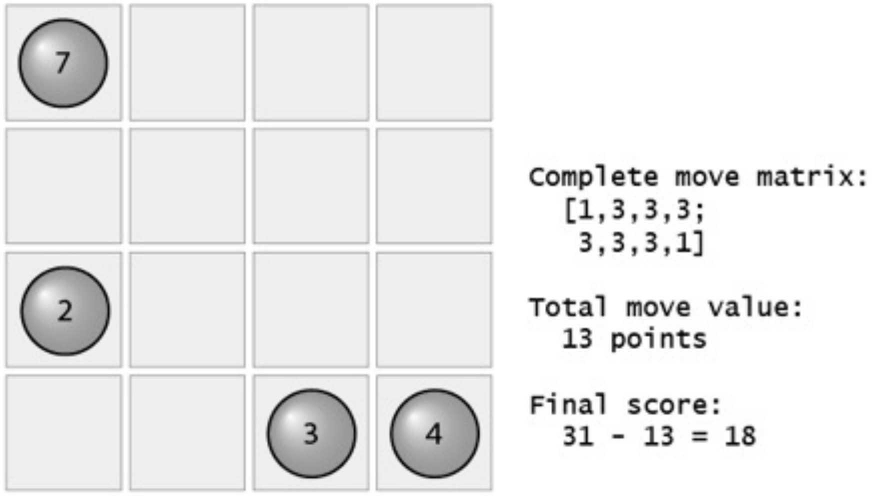
An example game



The initial score for this board is 31 (the sum of all the weights on the board). The removal bonus for this move is 8, and the penalty is 2, so the value of the move is 8 – 2 = 6 points. The score after this move is 31 – 6 = 25 points.



In move 2 there is no penalty, as we are using the same peg. The score after this move is 25 – 7 = 18 points.

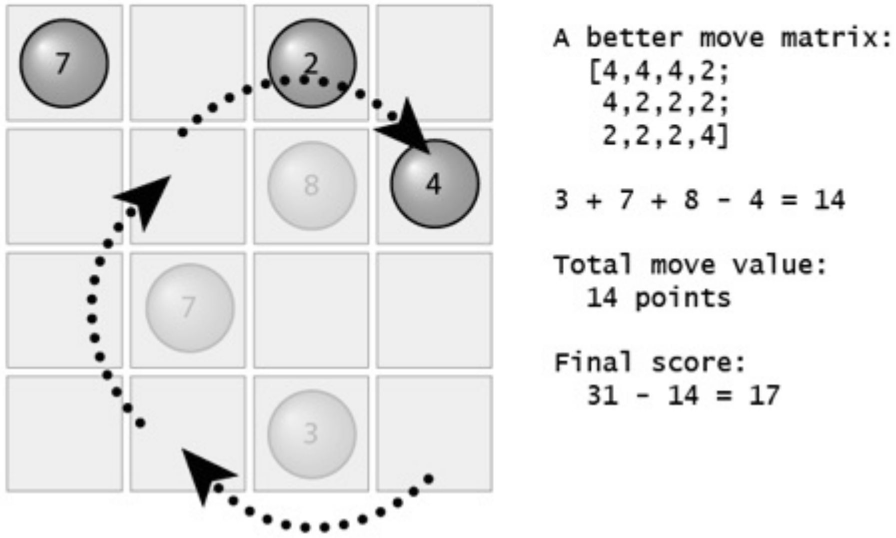


```
Complete move matrix:
  [1,3,3,3;
   3,3,3,1]

Total move value:
  13 points

Final score:
  31 - 13 = 18
```

At this point, there is no further move that will improve the score. The only move possible is jumping the 4 peg over the 3 peg, but since the jumping peg has a higher value than the peg being jumped over, this would not improve the score.



```
A better move matrix:
  [4,4,4,2;
   4,2,2,2;
   2,2,2,4]

3 + 7 + 8 - 4 = 14

Total move value:
  14 points

Final score:
  31 - 14 = 17
```

There is a slightly better alternative series of moves. Starting from the same initial configuration, the 4 peg can be used to jump over the 3, 7, and 8 pegs in succession. Although the first jump in disadvantageous, the overall result is better. The final score is 31 – 3 - 7 - 8 + 4 = 17 points.

Scoring

The overall score of an entry is a combination of three factors:

- result – the average score across all game boards
- runtime – how fast the code runs
- complexity – cyclomatic complexity - a measure of the number of independent paths through a program's source code. Typically, as this number gets higher, the program becomes less transparent and more difficult to understand.

The final score is calculated according to the equation:

$$score = k_1 * result + k_2 * e^{(k_3 * runtime)} + k_4 * max(complexity - 10, 0)$$

The goal is to minimize all three factors. The lowest overall score at the end of the contest wins. An entry is disqualified if it has a runtime over 180 seconds.

Data structure

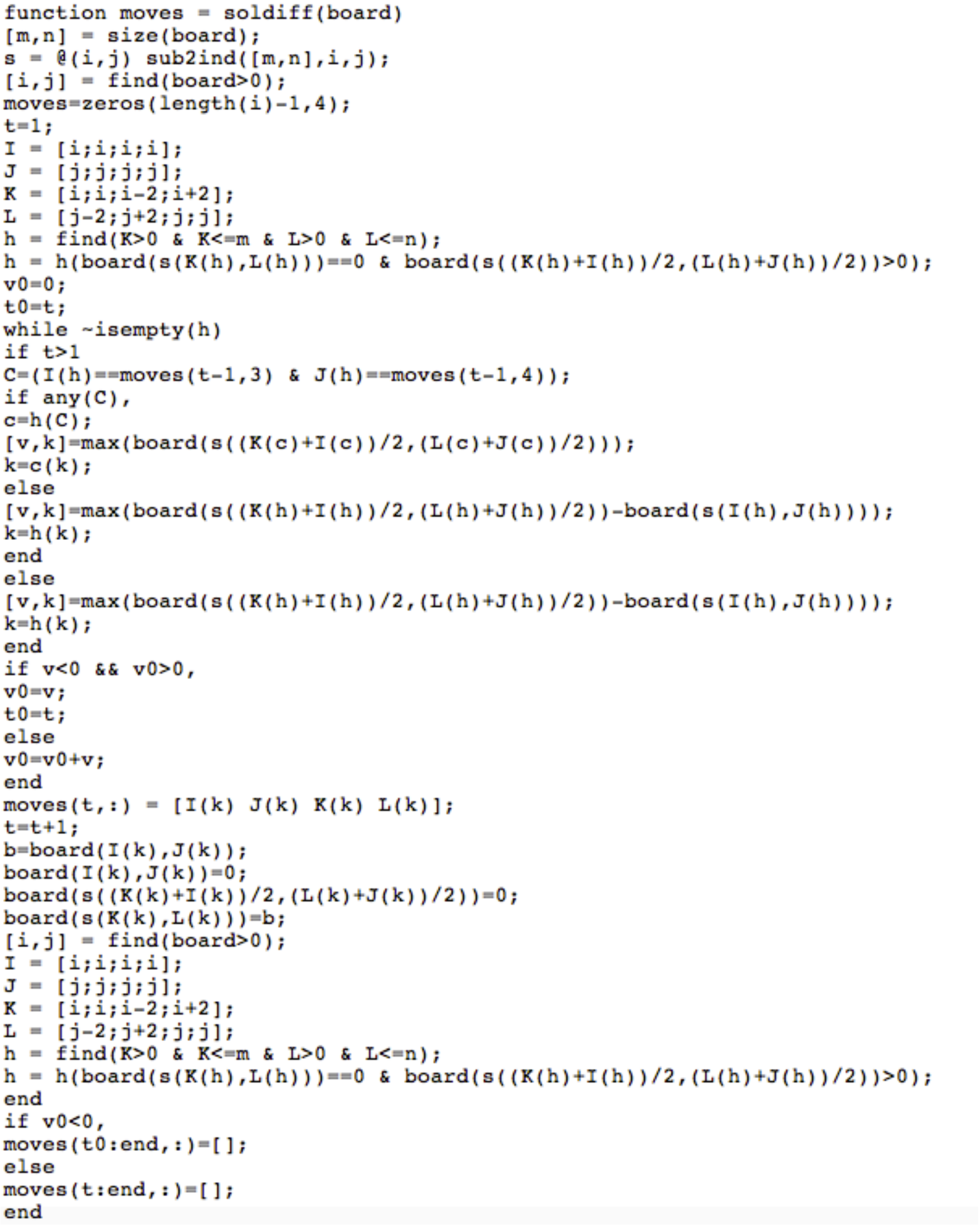
Meta data

For each entry in the contest, we have information on:

- the overall score
- the time of submission
- title of the entry
- a numeric identification of the author
- the result – the average score from solving the problems in the test set
- CPU runtime
- a numeric identification of the entry
- whether the author declared a parent entry as inspiration
- the rank of the entry at the time of its submission
- whether the entry passed the contest requirements
- the code, stored as a list of the lines

```
       score: 4.4839e+03
           t: 7.3317e+05
       title: 'LocalMinimum+depth'
   author_id: 17
      result: '44717.28'
         cpu: 36.1490
          id: 10665
      parent: NaN
initial_rank: 1
      passed: 1
       lines: [1x56 double]
   new_lines: [18825 18348 12725 18831 18348 18830 12703 15269]
```

Sample entry



```
function moves = soldiff(board)
[m,n] = size(board);
s = @(i,j) sub2ind([m,n],i,j);
[i,j] = find(board>0);
moves=zeros(length(i)-1,4);
t=1;
I = [i;i;i;i];
J = [j;j;j;j];
K = [i;i;i-2;i+2];
L = [j-2;j+2;j;j];
h = find(K>0 & K<=m & L>0 & L<=n);
h = h(board(s(K(h),L(h)))==0 & board(s((K(h)+I(h))/2,(L(h)+J(h))/2))>0);
v0=0;
t0=t;
while ~isempty(h)
if t>1
C=(I(h)==moves(t-1,3) & J(h)==moves(t-1,4));
if any(C),
c=h(C);
[v,k]=max(board(s((K(c)+I(c))/2,(L(c)+J(c))/2)));
k=c(k);
else
[v,k]=max(board(s((K(h)+I(h))/2,(L(h)+J(h))/2))-board(s(I(h),J(h))));
k=h(k);
end
else
[v,k]=max(board(s((K(h)+I(h))/2,(L(h)+J(h))/2))-board(s(I(h),J(h))));
k=h(k);
end
if v<0 && v0>0,
v0=v;
t0=t;
else
v0=v0+v;
end
moves(t,:) = [I(k) J(k) K(k) L(k)];
t=t+1;
b=board(I(k),J(k));
board(I(k),J(k))=0;
board(s((K(k)+I(k))/2,(L(k)+J(k))/2))=0;
board(s(K(k),L(k)))=b;
[i,j] = find(board>0);
I = [i;i;i;i];
J = [j;j;j;j];
K = [i;i;i-2;i+2];
L = [j-2;j+2;j;j];
h = find(K>0 & K<=m & L>0 & L<=n);
h = h(board(s(K(h),L(h)))==0 & board(s((K(h)+I(h))/2,(L(h)+J(h))/2))>0);
end
if v0<0,
moves(t0:end,:)=[];
else
moves(t:end,:)=[];
end
```

Contest information

Name	Date	Number of players	Number of entries	Number of passed entries	Total number of lines
Ants	**May 2005**	**167**	**2206**	**1972**	**18497**
Binpack	**Dec 1998**	**138**	**1455**	**877**	**6666**
Blackbox	**Nov 2006**	**170**	**6367**	**4600**	**85754**
Blockbuster	**Apr 2006**	**183**	**5922**	**5150**	**26546**
Color Bridge	**Nov 2009**	**117**	**2837**	**2270**	**14684**
Crossword	**Apr 2011**	**94**	**2280**	**1847**	**18362**
Gene Splicing	**Nov 2007**	**136**	**3285**	**2687**	**38760**
Gerrymandering	**Apr 2004**	**169**	**2392**	**2038**	**32749**
Mars Surveyor	**Jun 1999**	**63**	**1647**	**1371**	**10321**
Mastermind	**Sep 2001**	**123**	**1138**	**511**	**6322**
Molecule	**May 2002**	**154**	**1631**	**977**	**8286**
Moving Furniture	**Nov 2004**	**109**	**1834**	**1270**	**14282**
Peg Solitaire	**May 2007**	**119**	**3914**	**3426**	**19428**
Protein Folding	**Nov 2002**	**202**	**2437**	**1881**	**11901**
Sailing Home	**Nov 2010**	**98**	**3616**	**3175**	**17183**
Sensor	**Apr 2010**	**182**	**4814**	**4232**	**21503**
Sudoku	**Nov 2005**	**186**	**3061**	**2439**	**22778**
Tracking Freight	**Apr 2003**	**129**	**1661**	**1363**	**7369**
Wiring	**Apr 2008**	**106**	**4166**	**3707**	**92181**

Contest problem descriptions

Ants

In a sandbox with ants, sugar cubes, anthills, and rocks, try to bring back as many sugar cubes as possible back to the anthill in a limited time period, by using local information from each ant (limited vision, limited carrying capacity) while using chemical trails to guide ants across the sandbox.

Binpack

Given a list of songs and a CD length, try to find the best combination of songs that leave the least empty space on the CD.

Blackbox

Find out what is inside a black box by shining a laser into the box – the laser can be absorbed, deflected, or reflected, depending on how close is passes by the objects in the box, returning information about the objects.

Blockbuster

Given a box of coloured blocks, empty the box by ‘popping’ blocks – the block vanishes, so do all adjacent blocks of the same colour, and all the blocks above it fall down as though pulled down by gravity.

Color Bridge

A colour flooding problem – given a grid of coloured squares, create a four-connected single-colour region that reaches from the upper left corner to the lower right corner, by changing the colour of the top left square (two adjacent squares of the same colour will change colour together).

Crossword

Given a list of acceptable words, bearing weights, and a grid size, find a grid that maximises the number of high value words.

Gene Splicing

Based on the problem of gene transposition – given two DNA sequences, how many transposition events are required to transform the test sequence into the target sequence?

Gerrymandering

Carving up an electoral district according to population size in order to derive a political advantage – given a map grid with different population sizes in each square, divide the grid into N districts of roughly equal population.

Mars Surveyor

Program a mars rover – explore as much land as possible of a rectangular grid while avoiding obstacles, with limited fuel.

Mastermind

Iteratively guess an unknown sequence of coloured pegs given incomplete feedback in the form of black and white pegs, which indicate how many pegs are the correct colour in the correct position, or the correct colour in an incorrect position, respectively.

Molecule

Model the structure of a two dimensional molecule – given a list of lengths of linear rods connecting atoms, try to combine them as well as possible in a two dimensional shape.

Moving Furniture

Move furniture from one configuration to a second configuration with as little effort at possible (effort is defined as distance and weight of furniture)

Peg Solitaire

A modified version of a peg jumping game – on a board containing pegs and at least one empty space, pegs can be removed by jumping over them with another peg. Here, each peg carries a value, and the aim is to remove as many pegs with a combination of jumping moves while maximising the points collected.

Protein Folding

Simplified version of a protein folding problem in two dimensions, with two amino-acids. Given the amino acid sequence of a protein, determine a final "optimally folded" configuration, which minimises the free energy level.

Sailing Home

Navigate a boat on a grid between two points by managing the boat's velocity – this can be affected by the boat's motor or by wind speed at different squares of the grid – the goal is to try to minimise the motor usage.

Sensor

Try to reconstruct an image in terms of its uncompressed pixel values by requesting "compressed" sensor values, each of which is the sum of pixel values within the uncompressed image, while trying to minimise the number of requests.

Sudoku

Generalised Sudoku problem – given a partially filled grid and a list of numbers (there might be more numbers than the grid requires), fill in the grid so that each row, column, and region add up as close as possible to the same target sum.

Trucking Freight

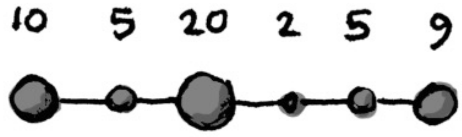
Variation of the travelling salesman problem – while driving a truck on a map populated with certain stations that contain either some amount of freight (a warehouse) or some amount of fuel (a gas station), maximise the amount of freight you can return to the base, while minimising the amount of gas.

Wiring

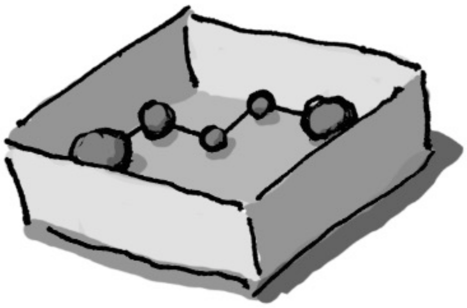
Inspired by the problem of wiring printed circuit boards – given a board with numbered pins, connect each pin to all other pins with the same number, while minimising the length of the connector wires.

The Chain Game rules

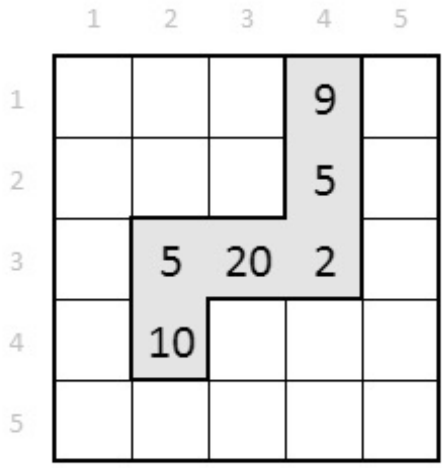
In this contest, you are given a chain and a box. Each link in the chain is exactly one unit long, but each one has a different weight. It looks something like this.



Your job is to place the chain in the box as compactly as possible. The constraint is that the chain must lie in a single plane and snake through the box using only straight segments or 90 degree turns.

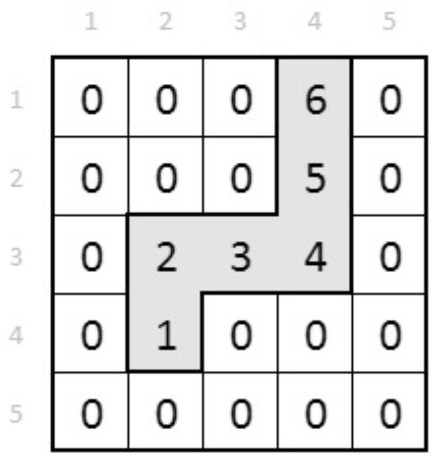


So for example, if you are given the chain vector c = [10 5 20 2 5 9] you might choose to put it into a 5-by-5 box like so.



	1	2	3	4	5
1				9	
2				5	
3		5	20	2	
4		10			
5					

If this is how you want to arrange the chain, your code would return a box matrix b like the one shown below. The first element of the chain, with weight 10, goes into row 4, column 2. The second element, with weight 5, goes just above it at location b(3,2), and so on.



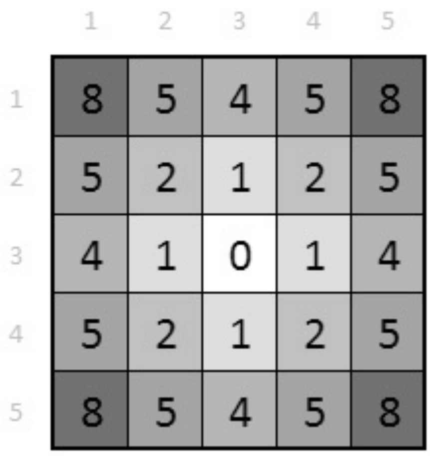
	1	2	3	4	5
1	0	0	0	6	0
2	0	0	0	5	0
3	0	2	3	4	0
4	0	1	0	0	0
5	0	0	0	0	0

Results

We will measure compactness by calculating the rotational moment of inertia around the center of the matrix. Physically you can imagine that we are putting the box on a turntable and spinning it. You want the box to spin with as little effort as possible. Mathematically, the moment of inertia is calculated by multiplying the mass of each link by the square of the distance to the center of the box matrix.

$$I_{rot} = \sum_n m_n r_n^2$$

In our simplified matrix problem, this means each position in the box has a penalty based on how far it is from the center. For a 5-by-5 box, this distance penalty matrix p looks like this.



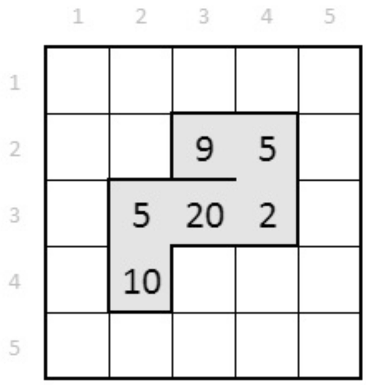
	1	2	3	4	5
1	8	5	4	5	8
2	5	2	1	2	5
3	4	1	0	1	4
4	5	2	1	2	5
5	8	5	4	5	8

The box is always a square matrix with an odd number side length n. So there is zero penalty for whatever link occupies the centre of the box. That makes it a good place to put your heaviest link, which is exactly what we've done here. Our result is thus

```
res = 10*2 + 5*1 + 20*0 + 2*1 + 5*2 + 9*5
```

res = 82

We pay a high price for the 9 in the first row of the box. Let's twist the 9 down to location b(2,3) as shown here.



	1	2	3	4	5
1					
2			9	5	
3		5	20	2	
4		10			
5					

```
res = 10*2 + 5*1 + 20*0 + 2*1 + 5*2 + 9*1
```

res = 46