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Multilevel Selection and Major Transitions in Sociocultural Evolution

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Abstract. There has been a growing literature on the applicability of abstract Darwinian principles to the sociocultural domain. In this paper, I will argue that the theoretical framework of multilevel selection and evolutionary transitions in individuality is applicable to human sociocultural evolution and that its application gives us great unificatory power. In order to do so, I will first provide a general account of major evolutionary transitions and their relation to the levels of selection in evolution. Next, I will defend the applicability thesis because the successive levels of social organisation in human societies satisfy the conditions required to fall under the set of explananda of the multilevel selection and evolutionary transitions framework; that this applicability entails the evolution of a certain type of traits at each successive level; and that at least some of these traits must be in some ways similar to traits involved in the evolution of biological levels of organisation; meanwhile attempting to link the conceptual to the empirical. Finally, I will explore the implications of this thesis.

Acknowledgements

This project grew out of my general interest in the topic of evolutionary transitions and multilevel selection, initially ignited by reading the works of John Maynard Smith and Eörs Szathmáry, Leo Buss, Richard Michod, Daniel McShea, and Samir Okasha during the last two years of my undergraduate education. First and foremost, I would like to thank Professor Okasha for the supervision he has kindly provided thus far on this (as well as an earlier related) project during my year here at University of Bristol's Philosophy Department. I would also like to thank Dr Jonathan Grose and Dr Tudor Baetu for their earlier mentorship on the philosophy of biology course here. I am also grateful to Professor McShea for expressing his view on the project, which I found to be very constructive.

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I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Taught Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, this work is my own work. Work done in collaboration with, or with the assistance of others, is indicated as such. I have identified all material in this dissertation which is not my own work through appropriate referencing and acknowledgement. Where I have quoted or otherwise incorporated material which is the work of others, I have included the source in the references. Any views expressed in the dissertation, other than referenced material, are those of the author.

SIGNED: DATE:

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Introduction.

The abstract nature of Darwinian evolutionary concepts.

My copy of Darwin's *Origin of Species* is, excluding the glossary and the introduction, 564 pages long. Darwin himself quite famously meant for the historic title to be the mere "abstract" of a much more substantial work. Quite fortunately, he never went through with that. If he had, however, we would have been faced with a plethora of facts supporting his view on evolution, perhaps several times the amount that is present in the *Origin*.

I am not a historian of science. Surely, Darwin must have had good reasons not to pursue the composition of that much larger work, of which I am not well aware. However, I can speculate to some degree, and I think the main reason was probably that he had in fact laid down the core of his theory in the *Origin*, buttressed by around 500 pages of real world empirical data. I contrast here the empiricity of the large buttress with the conceptual and abstract nature of the core of the work; the theories for which the data served as a buttress. As Darwin himself had been well aware, it is theory that holds together data, and data without theory amounts to nothing:

How odd it is that anyone should not see that all observation must be for or against some view if it is to be of any service. (Howard, 2001)

In other words, Darwin's view on evolution had landed already, and he did not necessarily have to provide much more evidence for it: his successors would be taking care of that. These include all the scientists who began to describe and explain disparate phenomena under a single theoretical framework: Darwinism.

But what is it about the Darwinian framework that makes it possible for this huge mass of seemingly unconnected data, from genetics to ecology, and from physiology to anthropology, to come under this highly inclusive theoretical umbrella? The answer is simply the extremely abstract nature of the most fundamental of the Darwinian principles; namely, evolution by natural selection. The abstraction lends generality to the theory because a highly abstract theory does not need to account for the idiosyncrasies of all the phenomena it attempts to explain, thereby potentially including a vast array of such phenomena in its set of explananda. In the case of the theory of evolution by natural selection, the high level of abstraction results from the small number of properties that a population of entities needs to possess in order to qualify as an explanandum for

the theory. Darwin discovered these properties, but did not extract them from his mass of empirical data. For that we have to thank his successors, most notably Richard Lewontin, who, among others, cites a few conditions for natural selection to occur (Lewontin, 1970):

1. Different individual in a population have different morphologies, physiologies and behaviours (phenotypic variation).
2. Different phenotypes have different rates of survival and reproduction in different environments (differential fitness).
3. There is a correlation between parents and offspring in the contribution of each to the future generations (fitness is heritable).

The generality that comes with this level of abstraction is often cited as the main reason for the astounding success of the theory of evolution by natural selection in unifying biology. As Dobzhansky (1973) once famously remarked: “Nothing in biology makes sense except in the light of evolution.”

But is the set including all the explananda of evolution by natural selection restricted to biology? There is certainly no *a priori* reason to think so. Phenotypic variation, differential fitness, and heritability of traits don't necessarily need a biological actualisation, just as they don't require any specific biological mechanisms for making them possible. Therefore, whether or not any non-biological phenomenon qualifies as an explanandum for the theory of natural selection should be decided in light of its properties; more specifically, whether or not it consists of a population of entities with phenotypic variation, differential fitness, and heritability of traits.

Examples of the attempts at the application.

One specific set of phenomena especially looks promising as a potential explanandum for the theory of natural selection, namely cultural evolution in human populations. That human culture has undergone evolution, in the broadest sense of the word, is out of the question. Evolution in this sense simply means change, and human culture has certainly changed from its humble beginnings to the tremendous complexity that we now see. It is another question, though, to ask whether the nature of this evolutionary change is Darwinian. Put another way, we might want to pose the question of whether human culture satisfies the most basic and the least restrictive conditions that were mentioned above, thereby undergoing natural selection. Whether or not this is the true is an

entirely empirical matter; it may or may not be the case. Moreover, the applicability of the most basic Darwinian principles in this way certainly does not entail that cultural evolution should be in every way analogous to biological evolution. This follows simply from the fact that how evolution by natural selection *actually* happens, i.e. what mechanisms underlie variation, differential fitness, and heritability, do not matter at the highest levels of abstraction. In other words, evolution by natural selection is multiply realisable.

The idea that the theory of natural selection is applicable to human culture is in fact not new. Darwin himself, in the *Descent of Man* (1888) hinted at the possibility of such an application by pointing out that if certain tribes have stronger propensities towards cooperation, they will likely compete more efficiently against other tribes who don't possess such properties. About a century later, Dawkins (1976) famously proposed memes as the cultural equivalents of genes: self-replicating entities that affect the phenotypic characters of human individuals in their own self-interests. Boyd and Richerson (1985, 2005) explore the role of gene-culture coevolution in the evolutionary history of humans. Hodgson and Knudsen (2010) attempt to formalise the application by identifying criteria for units of replication and selection, as well as taking the principles of evolution to a highly abstract level in order for it to accommodate the disparate domains of biological and social sciences. I will refer the reader to the same book by Hodgson and Knudsen for a more exhaustive list of evolutionary approaches to human culture and society since Darwin to the modern day.

Laying out the purpose of this paper: the applicability of the levels of selection framework to human evolution.

My aim in this paper is to argue that a slightly more restrictive set of conditions than those of natural selection are also met by human cultural evolution. This slightly more restrictive set is that which pertains to the theoretical framework that has been developing in evolutionary biology in the past few decades in order to explain phenomena such as altruism and the hierarchical nature of evolving biological entities. I will call this body of theory the levels of selection and evolutionary transitions framework. In order to argue for its applicability to human cultural evolution, I will start by providing a summary of its origins and development in modern evolutionary theory. This section will take up a considerable portion of the paper, as one of my aims for writing this paper is to reach a version of the framework abstract enough that it can accommodate the sociocultural

sphere as well as the biological. I will then lay out my main argument for its applicability by showing that human cultural evolution does indeed satisfy the set of conditions required for it to be an explanandum of the framework. I will then argue that this applicability entails the presence of similar traits in social organisations as can be found in biological systems that also fall under the theoretical framework, and that the actual presence of such traits in the cultural sphere would count as empirical support for the applicability hypothesis. Next, I will focus on the peculiarities of cultural evolution and how that affects the exact way in which the framework should be applied to this domain. Finally, I will recap my motivations for writing this paper as well as some of its possible philosophical and scientific implications.

1. History and review of the levels of selection and major transitions framework in evolutionary biology

The problem of altruism, Darwin, group selection, gene selection, Hamilton's rule, the Price equation and multilevel selection, the major transitions in evolution.

One of the most enduring and crucial debates in evolutionary biology that has lasted since at least the mid-twentieth century is the debate surrounding the interrelated problems of cooperation and conflict and the levels of selection. Though it has been a more explicit debate with its own literature since the 1960s, the ubiquity of cooperation and conflict in the biological world had inevitably drawn to itself the attention of biologists at least as early as Darwin himself. The debate stems from the theory of natural selection at the abstract level, and its core is as follows.

The theory of evolution by natural selection, as has already been mentioned, describes populations of entities which vary in terms of heritable traits which grant them fitness. It therefore predicts that entities which possess traits that make them act in their own interests should be favoured by natural selection, as they will have a greater contribution to the next generation. So far, so good. The problem arises when cooperative and altruistic¹ traits are taken into account. How will altruistic traits be selected for, when they decrease the fitness of their bearers? Given that individuals do in fact occasionally behave altruistically towards other individuals, there must be an evolutionary explanation for why altruism has not been weeded out by natural selection.

Darwin sought to resolve this problem by claiming that selection does not only favour individuals, but also groups of individuals (Darwin, 1859). He chose as his example a paradigmatic case of altruism among animals, namely honeybees. Honeybees, among other highly social insects, form highly integrated colonies with a high level of interdependence and division of labour between individual bees. Much of the individual bees' behaviour is certainly cooperative, and some of their behaviour is unquestionably altruistic. This includes their defence of the colony: honeybees

¹ I use the terms cooperation and altruism in the sense defined by Bourke (2011): cooperation in the broad sense includes both cooperation in the narrow sense and altruism. Cooperation in the narrow sense between two parties is an interaction where both parties benefit, whereas an interaction is altruistic when one party benefits at the expense of the other. From here on, I will use the term cooperation to mean it in the broad sense, unless otherwise stated.

inevitably die after stinging an intruder². On Darwin's account, such traits are still adaptive, though not for the individual bees, but for the colony as a whole. As stinging bees die, the colony is saved. Darwin makes a similar point about human societies³.

Ascribing to selection at higher levels than that of the individual⁴ in order to explain altruistic or cooperative behaviour remained common practice among biologists for about a century after Darwin (see Tinbergen, 1953; Lorenz, 1966). Wynne-Edwards (1962) sought to formalise such approaches in terms of what he called group selection. According to his account, selection acts at the group level when there is sufficient heritable variation in fitness among groups of organisms, which can then explain the emergence of altruistic traits among individual organisms. His work, however, was met with fierce criticism first by Williams (1966) and later Dawkins (1976), among others. The basic problem is that according to the critics of the group selection theory biological populations do not in fact satisfy the conditions required for group selection to happen. The main reason, according to the critics, is that mutation and migration, even at small rates, significantly reduce between-group variation, which in turn precludes selection occurring at the group level⁵. The criticisms differ in terms of their strength. While some are theoretically opposed to group selection altogether, others simply claim that group selection just does not happen in the real world for the reasons just mentioned.

But how to circumvent the altruism problem without referring to group-level selection? The critics of group selection are often grouped together as belonging to the gene-selectionism camp. The reason behind this is the fact that without the option to refer to group selection to explain altruism, one will have to resort to explaining it in terms of selection at the level of the genes (I will return to why this happens to be the case towards the end of the next section). This line of thinking is exemplified in the work of Hamilton (1964), which at the most basic posits that a gene for altruism will spread in the population if it satisfies the following condition:

² This is due to the fact that their stingers often get stuck in the intruder's skin, and once they fly off, their abdomens will be torn open and they will die shortly thereafter.

³ See section 2 of the introduction.

⁴ Levels in this sense is meant as hierarchical levels of organisation comprising part-whole relations between biological entities. Higher levels mean more inclusive levels. In the case of honeybees, the colony is the higher-level unit whereas the individual bees are the lower-level units.

⁵ This has been dubbed "tragedy of the commons" (Hardin, 1968). "Subversion from within" is a closely related term coined by Dawkins (1976).

$$rB > C$$

Here I use r to mean the relatedness coefficient, which is defined as the probability that any random allele possessed by the donor of the altruistic behaviour is identical by descent⁶ in the recipient. B is the benefit, in terms of fitness, to the recipient, while C is the cost to the donor, in terms of fitness.

What Hamilton's Rule, as the relation above is commonly known, expresses is basically that an altruistic behaviour is worth it as long as the benefits gained by it, multiplied by the relatedness coefficient, outweigh the costs incurred by it. But how does this solve the altruism problem? In other words, why should it be worth it for an individual organism to lose fitness to another organism? The answer is that if Hamilton's rule is satisfied, the gene for the behaviour will spread in the population anyway since r denotes the probability that the recipient of the altruistic behaviour also has the altruism gene. Put another way, if one takes the "gene's eye-view" (Dawkins, 1976), it doesn't matter which organism helps the gene reproduce. The gene spreads as long as some organism serves this function.

The significance of Hamilton's rule is that by shifting the focus of evolution to genes, it eliminates the need for explaining altruistic traits in terms of group selection, and seemingly does away with the problems associated with it. What it also entails, however, is that selection doesn't happen at the level of the individuals either. This sounds somewhat counter-intuitive, especially given that Darwin knew nothing of genes, and still came up with the theory of natural selection. Moreover, the conditions for natural selection to occur clearly hold for individual organisms, and there is no *a priori* reason to think that they cannot hold for groups.

Although there are ways to circumvent the problem (see Dawkins, 1976), I will turn my attention to the last point, which became especially relevant through the work of Price (1972). Price's equation is, simply put, a mathematical formulation of the most abstract conditions for natural selection. There are numerous ways that the equation can be expressed. One expression is especially intuitive when considering the possibility of selection occurring at more than one level, as it breaks down the selection to within-group and between-group components (Okasha, 2006).

⁶ Identity by descent (as opposed to identity by state) refers to situations where two given alleles in a gene pool are identical due to the fact that they are copies of the same token allele in a common ancestor.

This shows that group selection is at least possible in theory, as groups can in principle express heritable variation in fitness⁷. Therefore, the real question to answer would be to ask whether or not group selection happens in actuality.

One very important clue to whether or not group selection happens in actuality came from pointing out something that had for a long time been taken for granted, namely that the biological hierarchy could not have come out of nowhere. Up until the late 1980s, the debate over whether natural selection acted on groups, individuals, or simply their genes, did not explicitly take into consideration the fact that individual organisms *must themselves have started out as groups of lower-level entities*. Consider honeybees. In their case, the group vs. individual selection debate had historically focused on whether selection acted on individual bees, or colonies of bees. But individual bees—and multicellular organisms in general—have not always existed. Life started out as very simple. Depending on where we decide to draw the line between the living and non-living, the humble beginnings of life were either acellular or in the form of very simple cells. Either way, one thing is certain: unicellular life *must have* preceded multicellular life. In other words, multicellular organisms must have evolved from unicellular ones.

Another central idea of Darwinism, in addition to natural selection, is gradualism (Mayr, 1982). Gradualism in evolution basically means that evolution by natural selection does not produce adaptations abruptly⁸. This follows from the fact that most if not all variation acted upon by natural selection is random. Therefore most new variation is maladaptive, especially those that bring about significant phenotypic change. Natural selection picks out the few adaptive ones, which tend to be those with smaller effect on the phenotype. The evolution of complex multicellularity like that seen in bees from unicellular organisms takes a very large number of such small steps. In other words, it is far too improbable for it to happen abruptly. This brings us to the conclusion that multicellular organisms must have started out as groups of unicellular organisms, only gradually becoming organisms in their own rights (Buss, 1987). In order to see whether or not this entails selection at the group level, let's take a deeper look into transitions such as the evolution of

⁷ Though, this is not universally accepted. One might argue, for example, that since properties of the groups supervene on those of the individuals, selection at the group level is really just a by-product of selection at the individual level. See Okasha, 2006.

⁸ Note that the possibility of abrupt adaptive change is not ruled out by gradualism. It only asserts that such change is extremely unlikely.

multicellularity, collectively known as major evolutionary transitions or evolutionary transitions in individuality (though there is a subtle difference between the two, to which I will come back shortly).

Buss titled his 1987 book *The Evolution of Individuality*. This refers to the idea that during the evolution of multicellularity, on which Buss focuses, individuality at the level of the multicellular organism is something which has itself evolved. Buss attempts to explain this transition in terms of selection occurring simultaneously at two levels, namely that of the unicellular organisms and the groups of these organisms which gradually evolve into multicellular organisms. The argument seems to be that in order to prevent competition at the lower level from disrupting the stability of the higher level unit, certain adaptations are required to evolve. These adaptations include a life-cycle bottleneck, a germ-soma distinction, and policing mechanisms (Buss, 1987; Michod, 2000, 2005). The point is that these are adaptations of the higher-level unit; they only evolve when there is a higher-level unit involved, and are required in order for the higher-level unit to endure.

This way of thinking about things already hints to selection acting at the higher level throughout the transitions. This brings us back to the earlier dilemma: does selection occur at the level of the gene, or individual, or group? Are they mutually exclusive? There doesn't seem to be anything wrong with Hamilton's rule, and the explanatory power of fields such as behavioural ecology lend strong support to gene-selectionism. On the other hand, some form of group selection seems indispensable to explain at least the evolutionary transitions. Is there a way to reconcile the two views? Buss himself, in *The Evolution of Individuality*, is of the opinion that describing the transitions in terms of multilevel selection is equally valid as describing them in terms of gene-level selection. In other words, he seems to think that the debate is merely an epistemic one, and that explaining the transitions in terms of multilevel selection is simply a more efficient way of doing it.

On the other hand, Maynard Smith and Szathmáry (1995) seem to be more committed to a gene-selectionist view in their ground-breaking book *The Major Transitions in Evolution*. There they attempt to unify several evolutionary transitions under one rather abstract generalisation, namely that during these transitions the manner in which information is transmitted through generations undergoes a major change. Their list includes the evolution of cells, chromosomes, the genetic code, eukaryotic cells, sex, multicellularity, eusociality, and language. They hold that no matter

how the transitions progress, Hamilton's rule must be satisfied for genes. Cooperation cannot spread in the population if the genes for cooperation are at a selective disadvantage against other genes. Maynard Smith and Szathmáry also managed to provide a rather satisfactory account of the transitions without putting it in the language of multilevel selection. Though this is not strictly contrary to Buss's claim that the debate is essentially epistemic, it does seem to run against his other claim that multilevel selection theory is more efficient in explaining the transitions.

What are we to make of all this? To begin with, it's important to point out that more recent accounts of the transitions tend to distinguish between evolutionary transitions in individuality (ETIs for short) and other transitions on Maynard Smith and Szathmáry's list. The ETIs are essentially the ones that consist of new individuals forming at the higher level through the aggregation of former lower-level individuals, which includes the evolution of cells, eukaryotic cells, multicellular organisms, and eusociality. By virtue of this they fall under the theoretical umbrella that describes multilevel selection in a hierarchical setting with part-whole relations. The evolution of chromosomes, the genetic code, sex, and language are therefore excluded. Focusing on the ETIs, we can now make yet another distinction between replicator selection and interactor selection⁹. Here I define an interactor as the entity which has properties relevant to its fitness (adaptive traits) which, in interaction with the environment, significantly affects the probability that its component replicators will persist to the next generation. Examples of interactors include, but are by no means restricted to cells, multicellular organisms, and colonies of eusocial organisms (also known as "superorganisms"). A replicator, on the other hand, will be defined as the entity that is replicated in order to ensure that the interactor is produced in the next generation; and thus has a causal role in the production of the interactor¹⁰. The paradigmatic replicators in the biological world are genes (Figure 1).

The take-away from this way of defining interactors and replicators is that even though the interactor is (by definition) the entity that actually undergoes selection, the replicators will not only

⁹ There are instances of referring to the former as *selection of* and the latter as *selection for* (see Hodgson and Knudsen, 2010). However, I will avoid this way of referring to replicator and interactor selection because it is also used to describe situations where there is selection *for* a certain gene because of the effects it has on the fitness of an organism, as well as selection *of* another gene because it is in linkage disequilibrium with the gene that is being selected *for* (See Futuyma and Kirkpatrick, 2017).

¹⁰ The two definitions are basically simplified versions of those used by Hodgson and Knudsen (2010).

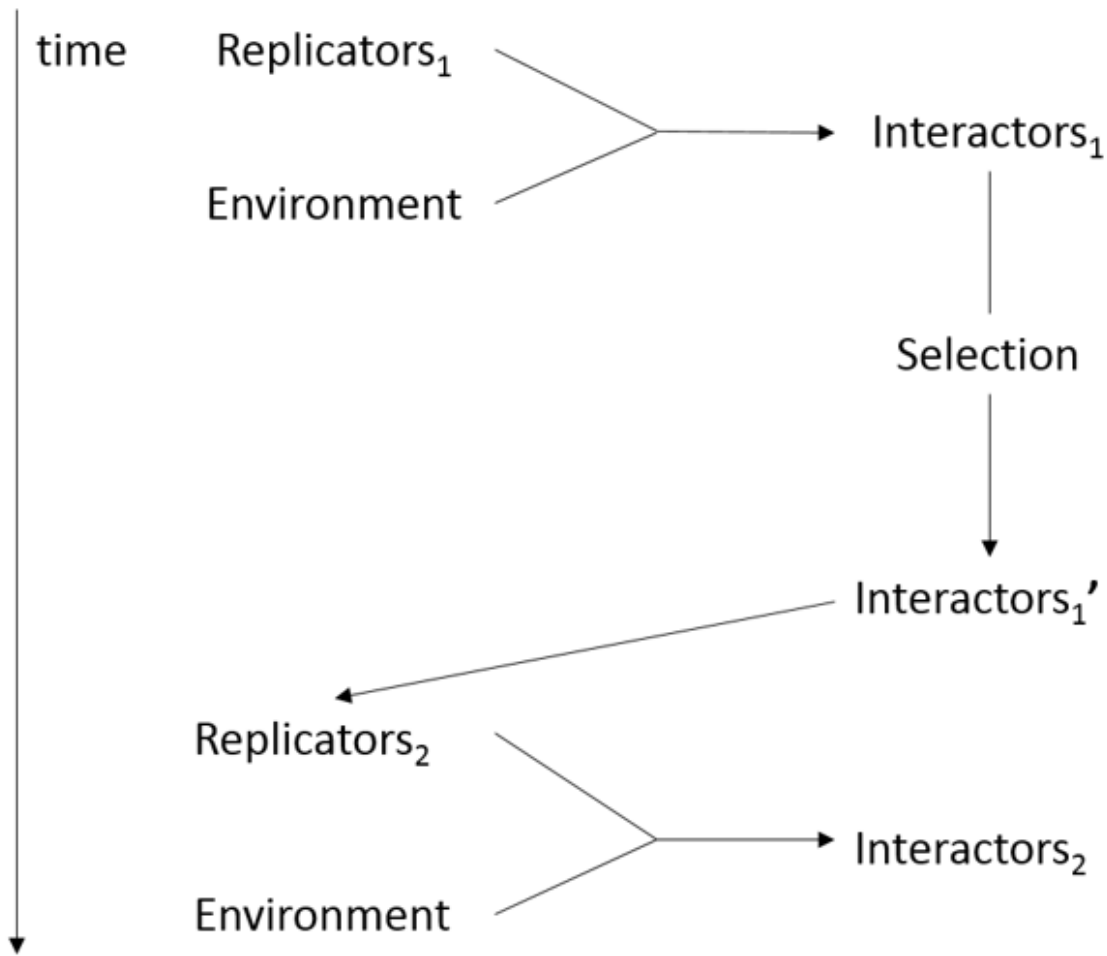


Figure 1. With interactors defined as the bearers of adaptations, selection in the sense of the differential survival and reproduction of entities bearing adaptive traits must happen to them. Replicator selection is inescapable as interactors themselves have no way of producing the next generation of interactors (interactors₂). Bear in mind, though, that the distinction is merely conceptual: entities can be both interactors and replicators simultaneously.

also appear to be undergoing selection¹¹, but it will appear as if the replicators undergo a more essential kind of selection: hence the fact that in each transition, the satisfaction of Hamilton's rule seems to be unavoidable. In order to see why this is so, consider the fact that in figure 1, the

¹¹ This might explain why replicator selection has been referred to as *selection of*, and interactor selection as *selection for*.

interactor can in principle be a hierarchy of levels, and thus decomposable into several subsets¹², whereas the same cannot be done with replicators¹³.

The conclusion to be made is thus that multilevel selection and gene-selection are not in fact two sides of the same epistemological coin, neither are they irreconcilable: multilevel selection seems to deal with interactor selection, whereas gene-selection seems to deal with replicator selection. This is because the interactors are the entities that can be organised in hierarchical levels with part-whole relations between them. This conclusion can also explain why the gene's eye-view has been described as a useful heuristic and a way of bookkeeping rather than "seeing" actual selection (Mayr, 1963; Sober, 1984; Gould, 2002; Okasha, 2006). ETIs are therefore the proper explanandum of multilevel selection, rather than gene-selection¹⁴.

The abstract nature of multilevel selection; the general account of major transitions/evolutionary transitions in individuality.

Given the conclusion reached at the end of the last section, what then do the ETIs exactly constitute? As already mentioned, ETIs are events during which individuals at a given level evolve out of the aggregation of individuals at the immediately lower level. But this in itself requires a definition of individuals. Here I will propose a slightly modified version of Clarke's (Clarke, 2010, 2016) definition of biological individuals. According to Clarke, a biological individual should be defined in terms of its capacity to undergo selection, rather than by virtue of possessing any specific traits. This is to say that the possession of traits such as a germ-soma distinction or a life-cycle bottleneck are not essential to biological individuality. However, Clarke also acknowledges that in order for selectability (and therefore individuality) at a given level to persist, *some* such traits need to be present. Clarke calls such traits *individuating mechanisms*, and I will stick with this term throughout the paper. Clarke's account of biological individuality is therefore a highly abstract one, where biological individuality is multiply realisable.

¹² Note that I take the interactor to be a set of all properties relevant to fitness. While the actual entity will certainly have other properties, they can safely be ignored, as they have nothing to do with selection. Similarly, it is easily possible for the interactor and the replicator to be the very same entity (for example self-replicating RNAs early in the history of life on Earth which also had enzymatic functions). The conceptual, definitional difference is what matters in this context.

¹³ This sounds somewhat similar to Godfrey-Smith's distinction between simple and collective reproducers (Godfrey-Smith, 2009).

¹⁴ This is not meant to undermine the significance of gene-centred research on ETIs. Genes are the replicators of the biological world, and the evolution of adaptive traits can be conveniently traced through their evolution.

There are a few points to be made here. First is that Clarke's definition of a biological individual has one minor setback: it is somewhat too permissive about what qualifies as an individual. By her account, even very loosely defined groups that undergo *some* selection qualify as *something* of an individual. This is slightly counter-intuitive, since an "individual" is otherwise intended to imply a rather well-defined entity. Put another way, Clarke's account lacks proper demarcation criteria for individuality. My proposal is that individuals should be defined as a subset of interactors; more specifically, those interactors that are quite clear-cut and well-integrated¹⁵. This solves the problem of the high permissiveness of Clarke's definition of individuals.

The second point is that the highly abstract nature of this account, and the highly abstract account of ETIs that it entails, make it applicable to a wide range of phenomena, in the same manner in which the highly abstract nature of the theory of natural selection does the same¹⁶. This potentially includes transitions both of the egalitarian and fraternal kinds¹⁷, and transitions at different levels. But the ETI criteria in this account is so highly abstract that it could, in principle, also apply to non-biological transitions, which is the subject of the next chapter.

The third point is that the individuating mechanisms required for a transition to proceed need to have certain functional properties. According to Clarke, they need to either suppress selection at the lower level (policing mechanisms), or enhance selection at the higher level (demarcation mechanisms)¹⁸. In the biological world, these include the germ-soma distinction, life-cycle bottlenecks, various sorts of division of labour, and so on. Thus, if the account is indeed applicable to transitions in non-biological domains, similar such traits should also be found.

The final point has to do with higher-level adaptations other than individuating mechanisms. To demonstrate this point, I will first slightly modify Clarke's account of individuality once again: while Clarke defines the individual in terms of the capacity to undergo selection, I will define it in

¹⁵ I will refer the reader to the account of an interactor described by Hodgson and Knudsen (2010) for a definition of cohesion. I will expound on the relation between interactor in their sense and interactor and individual in the sense defined here later in this paper.

¹⁶ Needless to say, the set of all the explananda of the former is a subset of the set of all the explananda of the latter.

¹⁷ Egalitarian transitions are those in which genetically unrelated individuals form a new individual, such as the evolution of the eukaryotic cell. Fraternal transitions are those where genetically closely related individuals come together to form a new individual, such as the evolution of eusociality. See Queller, 1996 [was it?].

¹⁸ Though there is no *a priori* reason why any mechanism should not be able to satisfy both criteria, and Clarke does take this point into account.

terms of the possession of adaptations. The latter entails the former, but not the other way around. To see why this is true, and why they are not coextensive, consider the case of infertile hybrids such as mules. While mules certainly bear adaptations, they do not have the capacity to undergo selection, due to their infertility¹⁹.

Now that individuality has been defined in terms of the possession of adaptations, the question arises as to whether or not all adaptations are equally crucial to the evolution of higher-level units. We have already seen that individuating mechanisms indeed are crucial. The question can therefore be put in the following way: are all higher-level adaptations individuating mechanisms? The answer is certainly no. A paradigmatic counterexample would be wings. Wings have nothing to do with policing or demarcation. However, some adaptations might be related to individuation insofar as they have a role in the integration of the higher-level unit, which is accompanied by the increasing interdependence of lower-level units. This class of adaptations includes things such as centralised information processors (like brains), systems for transferring materials within the unit and across its boundaries (respiratory and circulatory systems), and determinate development; though it is unlikely that the list ends here. Despite their role in individuation, it's hard to classify these adaptations as individuation mechanisms in the strict sense defined by Clarke, as they are neither policing nor demarcation mechanisms: they are not mechanisms that have evolved for the means of conflict resolution. We are thus left with no choice but to admit that there is no strict delimiting point for what counts as an individuating mechanism and what doesn't. However, two things are certain: (1) this set of mechanisms can be categorised as non-reproductive division of labour, and that (2) they become more relevant during the later stages of a transition. The importance of this point becomes relevant in the third chapter, where the potential equivalents of these adaptations are considered²⁰.

In the next chapter, I will argue that the generalised account of the ETIs just described applies to a certain aspect of human sociocultural evolution, and explore what it entails in terms of

¹⁹ The case of infertile hybrids has been presented as an objection to Clarke's account (Stern, 2015). This modification solves the problem.

²⁰ A related line of thinking about the evolutionary transitions, which can be found in the work of Bourke (2011), among others (Bonner, 2006; McShea, 1996; Grosberg and Strathmann, 2007; Herron and Michod, 2008). Bourke (2011) describes a "complexity syndrome" that arises as a transition progresses. The components of this syndrome are a life-cycle bottleneck, reproductive division of labour, non-reproductive division of labour, and policing.

individuating mechanisms in the broad sense. I will argue that the actual presence of such mechanisms, especially in the strict sense (as they are more relevant) provides empirical support for the applicability of the theory to that domain. I will also attempt to bring examples of some possible interactors in that domain, as well as some candidates for individuating mechanisms. Finally, I will make a distinction between this way of thinking about the human sociocultural evolution in terms of evolutionary transitions and that developed by Hodgson and Knudsen (2010).

2. The application of the evolutionary transitions framework to human sociocultural evolution

The framework is applicable because (1) it is fundamentally abstract enough; and (2) the same multilevel structure is present in human societies.

In this section, I will lay out the core argument of this paper, which is that the multilevel selection framework is applicable to human sociocultural evolution. What this means is that human societies satisfy the set of criteria which makes them qualified as explananda of the multilevel selection framework; this set of criteria includes and is more stringent than the set of criteria for something to be an explanandum of the theory of evolution by natural selection. In other words, the multilevel selection framework is more restrictive in its scope than the theory of natural selection. Nonetheless, it's still quite abstract. Here I will denote a minimal set of criteria needed for an evolving population to fall under the set of explananda of the framework. My aim is to show that human sociocultural evolution does indeed meet these criteria, and therefore the framework is applicable.

The first condition is that the structure of the evolving population needs to be such that one class of evolutionary entities must be composed of (at least)²¹ groups of another class of such entities. In other words, the population needs to have a multilevel structure, with part-whole relations between entities at the two levels. There needs to be at least two levels, though there is no *a priori* reason why there couldn't be more. The higher-level entities may be so well-defined that they may rightfully be called individuals or units of selection, or they may only be relatively loose aggregations of the lower-level entities. All that matters is that the entities in question display adaptive traits pertaining to their level, and therefore bear fitness (bear in mind that this is strictly interactor fitness, as opposed to replicator fitness).

The second condition is that the fitnesses of the higher- and lower-level entities have the capacity to be aligned with each other, as well as being in conflict with each other. This condition is in fact a natural consequence of the first condition, given that the functions of different adaptive properties

²¹ This is an important point which is often overlooked: evolving higher-level entities don't need to be exclusively composed of evolving lower-level entities, other, non-evolving things are often involved as well. A multicellular organism, for example, does not exclusively consist of cells. A lot of it is made up of non-living material, such as the ECM in animals or wood in plants.

which can belong to either class of entities can very easily—though not necessarily—be at odds with one another. Put another way, with any set of two or more interacting evolutionary entities, the functions of the adaptations of any entity can increase, be neutral to, or decrease the efficiency of the functions of the adaptations of another entity in the set. This lies at the heart of conflict and cooperation among evolutionary entities, which is in turn crucial to the understanding of multilevel selection scenarios and ETIs.

What follows from these conditions, i.e. the presence of a system subject to multilevel selection, is that there must be a certain class of adaptations involved when an ETI is taking place. This class of adaptations includes, in the biological domain, the oft-mentioned reproductive division of labour, life-cycle bottlenecks, self/non-self recognition, etc. As already mentioned, the role of these adaptations is to limit selection at the lower level or enhance selection at the higher level. They achieve this by either aligning the fitnesses of the entities at the two levels, or by simply disabling the entities from achieving their fitness interests²². Thus, if the multilevel selection and ETI framework is applicable to the human sociocultural domain, the same kind of traits must be found there as well.

There are two points that need to be kept in mind, however. One is that the traits that would carry out this role in the human sociocultural sphere need not be the exact same traits that do so in the biological sphere. What this means is that the paired functions of reducing selection at the lower level and enhancing it at the higher level²³ can be potentially realised through various means, which can be vastly different in the two spheres; although there is good reason to think that they should be similar in important respects, as they are meant to play a similar role after all. What it also means is that as in the biological domain, none of these traits is essential for the selectability of the higher-level entities on its own. Rather, the selectability of the higher-level entity is also multiply realisable through different combinations of such adaptations.

²² This distinction is often not much emphasised in the literature, and deserves more attention. It is perhaps the equivalent of coercion in the biological literature. It seems to be play a more important role in the human domain, as I will elaborate in the third chapter.

²³ In Michod's (2005) terms, the transfer of fitness.

The second point is that if such traits are indeed found in the sociocultural domain, they will count as evidence for the applicability hypothesis. This simply follows from the fact that the hypothesis entails and therefore predicts the presence of such traits.

The next task would then be to show that these minimal conditions hold for human sociocultural systems. This can be subdivided into (1) showing that there are indeed entities in the sociocultural sphere that form evolving populations with a multilevel structure; and (2) that the fitnesses of these entities can be aligned or at odds with one another. We can then attempt to find examples of individuating mechanisms (fitness-trading traits) in the sociocultural sphere, which will provide empirical evidence for the applicability hypothesis. I will devote most of the rest of this chapter to these tasks.

Let us now turn to the first task, which is to show that there are populations of evolving entities in human societies that are hierarchically organised (i.e. are in part-whole relations). To do that, we need to identify possible such entities. The entities to look for should not only be interactors in the sense defined earlier (entities that bear adaptive traits and therefore affect the success of their component replicators in making it to the next generation), but they should also be members of that subset of interactors which form cohesive units. This subset was dubbed “individuals” in the biological sphere; though the term individual normally refers to single (individual) human persons in the sociocultural sphere, and is therefore best avoided in the meaning prescribed to it earlier. I suggest that the term “unit of selection” be used to refer to both biological individuals and cohesive interactors in the sociocultural domain. This is contra Hodgson and Knudsen [cite], who use the term interactor to refer to units of selections in the sense just defined.

The reason why we should look for units of selection, rather than any interactor, is twofold. Firstly, non-cohesive interactors, such as many insect or cnidarian colonies, or not-too-interdependent mutualist associations, are hard to identify and delimit by virtue of their lack of strong cohesiveness. Secondly, it is likely that studying the cohesive interactors could give us more explanatory power when it comes to evolutionary scenarios. An example from the biological domain would be that it is much easier and more informative to explain the evolution of mutualisms in terms of the fitness benefits of the individuals involved in the interaction than in

terms of fitness benefits to the mutualist association. The latter is often very loosely defined and its relation to the success of replicators is highly likely to be unclear²⁴.

Hodgson and Knudsen (2010) use their set of criteria for an “interactor” (unit of selection in the terminology of this paper) to identify several such entities. The set includes, but is most likely not restricted to, individuals, families, tribes, states, business firms, universities, and trade unions (Hodgson and Knudsen, 2010). I will not expound on how the entities satisfy the necessary conditions, and will refer the reader to the original account. I will point out, however, that these entities do in fact stand in part-whole relations to each other: individuals are parts of families, universities, and business firms, families parts of tribes and states, universities parts of states, and business firms parts of trade unions. This, in addition to the fact that the fitness interests of these entities can be aligned or at odds with one another, results in the applicability of the multilevel selection framework to human sociocultural evolution.

²⁴ It is tempting to think that this is exactly the reason for the success of such fields as behavioural ecology, which avoid group-selectionist models.

3. How the framework applies: how the abstract connects with the concrete

As pointed out in the introduction, the application of Darwinian principles to the sociocultural domain does not imply that sociocultural evolution must be in every way analogous to biological evolution. In other words, the details of *how* evolution happens in one does not have to be the same as that in the other. The same principle holds for the application of the multilevel selection framework to sociocultural evolution: only the most abstract features of multilevel selection and ETIs here need to be the same as those in biological multilevel selection and ETIs. In this chapter, some important differences between the two domains are considered, as well as the ways in which they can affect theorising about sociocultural evolution. I will draw mainly from the works of Hodgson and Knudsen (2010) and Boyd and Richerson (1985; Richerson and Boyd, 2005).

Humans as both biological and cultural interactors.

The most fundamental difference between the multilevel structures in biology and human societies, is perhaps that there is only one chief replicator²⁵ in the biological domain, whereas human societies harbour more than one kind of replicator. A recent account of various replicators in the sociocultural domain is given by Hodgson and Knudsen (2010), where they introduce the replicators in the context of “major information transitions” in cultural evolution. Their proposed replicators include corporeal habits, linguistic habits, customs, writing systems, laws, and scientific and technological knowledge. I do not aim to scrutinise their account, as my main concern here is with interactors rather than replicators. However, there is something important here that should be pointed out.

Hodgson and Knudsen explicitly point out that their account of “major transitions” is modelled after that of Maynard Smith and Szathmáry (1995). This means that they are most interested in transitions where a major change happens in the way information is transmitted through generations. Even though it is not clear how the emergence of new replicators would mirror

²⁵ The possibility of other replicators cannot be entirely ruled out, and some authors have indeed suggested that things such as centrosomes (more precisely Microtubule Organising Centres or MTOCs) may in fact be replicators in their own rights (Margulis, 1970, 1981). Recent work on developmental plasticity and the role of environmental factors in producing the phenotype (West-Eberhard, 2003; Gilbert and Epel, 2009) seems to suggest the role of at least some environmental factors as replicators in the sense described here. I believe this issue deserves further attention.

Maynard Smith and Szathmáry's account, as the replicators in their major transitions are invariably genes, there thus seems to be two similar dichotomies here. One has already been mentioned: that between ETIs and the major transitions captured by Maynard Smith and Szathmáry; while the former strictly deals with the emergence of new interactors, the latter is concerned with changes in the way information is transmitted. Similarly, the account I am trying to construct in this paper is meant to deal with the emergence of interactors, while Hodgson and Knudsen's account is concerned with the emergence of new replicators (which is presumably analogous to changes in the transmission of information). I am not trying to undermine the significance of an account of transitions in human sociocultural evolution that is most concerned with replicators; rather, my point is that the dichotomy between the two kinds of accounts needs to be clarified to avoid potential sources of confusion.

The existence of “r” substitutes, sense of identity, and how they relate to aligned interests of the interactors.

As mentioned earlier, Hamilton's rule describes situations where altruistic traits can spread in the population. This can be explained by replicator selection: the gene for altruism can spread if it gains a net benefit from the altruistic trait, which can be realised by altruistic individuals behaving altruistically towards other individuals who share the same gene. This can in turn be realised via different mechanisms; the individual can direct its altruistic behaviour towards those individuals with which it has grown up, those in its vicinity, or those that bear chemical signals that indicate kinship (Krebs, Davies & Parr, 1993). These are often indeed the individual's close kin, and the individual behaves altruistically towards its kin because they are most likely to carry the genes for altruism as well (hence the term kin selection).

Hamilton's original formulation, however, does not require kinship. All it needs is a positive correlation between the phenotypes of the donors (of the altruistic behaviour) and the genotypes of the recipients (Okasha, 2006; Godfrey-Smith, 2009). In other words, all that is needed for cooperation to evolve is positively correlated interactions between the entities. One way to realise this in the biological world is by directing cooperation and altruism towards kin, although other

phenomena such as reciprocal altruism (Trivers, 1971) or the green-beard effect essentially achieve the same thing.²⁶

Non-randomness of cooperative interactions between evolutionary entities seems to be a necessary condition for the evolution of higher-level interactors. In the absence of correlated interactions, the evolution of the higher-level unit will be thwarted by the tragedy of the commons²⁷, where the selfish tendencies of the lower-level units destabilise the groups. Therefore, this non-randomness must somehow be actualised in sociocultural selection too.

This last point is actually not a novel realisation, and finding out what actually keeps human groups²⁸ from falling apart has been discussed extensively in the literature (Sober and Wilson, 1999; Boyd and Richerson, 1985; Richerson and Boyd, 2005). The main question here is, as with biological evolution, how cooperation evolves in human groups. The other side of this coin is the question of how human groups deal with the problem of cheaters (or free-riders), or in other words, how cooperation is maintained. The answers include, but are not exclusive to, kin selection and various kinds of reciprocity to the collective punishing of cheaters and biases towards conformity with the group. While it is possible to discuss in detail how these mechanisms achieve their function, the limits to the scope of this paper prohibit such a discussion. However, there are a few notable points here that strongly pertain to the thesis presented in this paper.

The first point is that each of these traits can only be advantageous to their relevant replicators, i.e. the replicators responsible for producing them. This is due to the fact that a cooperative trait needs to direct its fitness benefits to the replicator producing it in order for that replicator to have a selective advantage against other replicators. Also, bear in mind that not only can a trait be the product of different tokens of a kind of replicator, e.g. a set of genes, but it can also be the product of different kinds of replicators. An example would be tribal loyalties, which is likely a result of both genetic, kin selection-related replicators (since tribe members are often closely related), as well as cultural replicators that pertain to the tribe.

The second point is that most such mechanisms have something crucial in common with respect to how they work: they make use of identity markers. Recall that all cooperation mechanisms need

²⁶ For a more elaborate discussion, see Godfrey-Smith (2009).

²⁷ See footnote 5.

²⁸ Any higher-level interactor.

to ensure that cooperation is directed towards other co-operators, in order to create the positive correlation that is required for the cooperation-generating replicator to evolve. Identity markers are a common, though not necessary, means of achieving this goal²⁹. Identity markers in the biological world are quite diverse, and range from cell-surface proteins to scents and auditory signals. In the human world, cultural identity markers are abundant in addition to biological markers, and these range from language, various forms of art, food, clothing, etc. Note that such vast phenomena can all qualify as identity markers because the criteria for being an identity marker, in the functional sense described above, are highly permissive: all that is needed is that they increase the probability that cooperative behaviour will be directed towards their bearers, and that their replicators be strongly correlated with the replicators for the cooperative behaviour itself³⁰. Also note that their role as identity markers need not be their only role, or the reason why they exist in the first place. Rather, they can be co-opted as such. Moreover, one kind of identity marker can be used as a proxy for another kind. An example that illustrates both these points is the association made by humans between physical features of humans and their culture. In such cases, a type of identity marker that was originally meant to be associated with genetic replicators becomes associated with cultural replicators, hence acting as a proxy by being co-opted³¹.

The third point has to do with the progression of successive transitions and the need for new individuating mechanisms to evolve in order to make them possible. Mechanisms such as tribal loyalties, for example, become obsolete in the context of large empires. The underlying cause here is, as with biological transitions, the increasing potential for conflict of interests as new higher levels emerge. This in turn is often (though not always) associated with size, defined in terms of the number of lower-level units in an emerging higher-level unit; this is especially true in fraternal biological transitions, but doesn't apply as neatly to egalitarian transitions (Bourke, 2011). While the extent to which size (in the sense defined here) has a role in the increase in potential conflict in various sociocultural transitions remains to be seen, the interests of hierarchically organised interactors are bound to be potentially at odds, which will require the evolution of new

²⁹ Positively correlated interactions can arise under conditions where the non-random association of interactors is ensured by limited mobility or by the offspring sticking together. In such cases, it is sufficient for the interactors to direct their cooperative behaviours towards other interactors in their proximity. Identity markers are therefore not necessary.

³⁰ A minimally sufficient example is the green-beard effect (Dawkins, 1976).

³¹ At least in today's world, such associations seem to persist when they are no longer particularly relevant, potentially giving rise to racism and other similar phenomena.

individuating mechanisms. Potential candidates for mechanisms at higher levels include new moral and legal systems, as well as religions and ideologies³² (bear in mind, though, that such mechanisms also rely on identity markers to function). A more careful analysis is needed to determine whether or not the candidates just mentioned qualify as individuation mechanisms, but that is beyond the scope of this paper. As already mentioned, they will count as evidence for the applicability hypothesis if they do in fact qualify as such.

The role of emotions and the exaptation.

Delving a little deeper into how individual humans and other sociocultural interactors come to actualise the positive correlation between cooperation and replicators generating the cooperative behaviours, the question poses itself of how humans learn to direct their cooperation towards other co-operators, or how they undertake the functions of individuation mechanisms. A related question to ask is how these interactors develop into their specific roles, i.e. how division of labour is actualised in human societies. Yet another related question has to do with evolution rather than development: given that individual humans are the basic units comprising interactors at every level, how did the cooperative behaviours of these individual humans originally meant for groups no larger than tribes evolve into those relevant to much larger interactors in spite of little if any genetic change? The same evolutionary question can also be asked about division of labour in the sociocultural domain as well.

The detailed answer to the first question certainly lies in the field of psychology, on which I am not literate enough, which together with the limited scope of this paper precludes providing such an answer here. However, one thing is clear: the learning mechanisms involved here need to have the essential property of being able to identify the individuals bearing the relevant identity markers, and increase the disposition of the individual towards cooperating with those bearing the markers. Furthermore, the markers identified by the mechanisms involved should not be limited to markers signalling kinship. This is due to the fact that humans do not only cooperate with their kin—as mentioned earlier, genetic replicators are not the sole class of replicators in the sociocultural world. Put another way, since cooperation with "cultural kin" (being the result of cultural cooperation

³² Hodgson and Knudsen (2010) regard the emergence of law as the emergence of a new kind of replicator.

replicators) is a ubiquitous feature of human societies, the cognitive apparatuses involved in human cooperation *must* allow it; it would otherwise not be actualised.

Another plausible important general feature of these mechanisms is that they are emotional in nature. This assumption relies partly on a Humean view of human nature, whereby human behaviour is motivated mainly by desires (Sinhababu, 2017), and partly on a body of anecdotal evidence regarding how the opinions of humans towards their genetic and cultural kin, as well as the higher-level units that they comprise (such as tribes, states, etc.) are emotionally charged. Perhaps the best place to look for this body of anecdotal evidence is in the various forms of arts and literature that concern things such as familial ties, tribal loyalties, personal duties, or "altruism" in general. Needless to say, such emotions can be aligned or at odds, as they are meant to track the interests of the various interactors at several levels, which can in turn be aligned or in conflict. Yet another plausible feature of these mechanisms, which is closely tied to their emotional nature, is that they often have a strong element of imprinting in them: we often learn the meaning of various identity markers³³ during early development, and they become less amenable to change as we age³⁴.

In the preceding paragraphs, I have mainly dealt with a "developmental" problem; i.e. how individuals learn how to actualise the positive correlation between cooperation and cooperation-generating replicators. But as mentioned above, there is a related "evolutionary" problem: given that we started out with kin-groups and almost exclusively genetic cooperation-generating replicators, our learning mechanisms involved in kin identification and the directing of cooperation must have been exclusive to genetic kin identification. How and at what point did they become able to accommodate the identification of cultural kin during our evolution?

Once again, I do not aim to provide a detailed description of the how and when for an answer. Rather, I aim to point out some general features that this evolutionary change has most plausibly had, and once again I will rely mainly on anecdotal evidence for support. As with other claims for which I have relied on such evidence, the path to providing empirical support is wide and open; although it will require much expertise and considerable effort.

³³ In terms of what they signal regarding what groups the individuals bearing them belong to.

³⁴ Again, I can only provide indirect anecdotal evidence for this claim: religiosity and patriotic feelings, for example, are commonly held to be harder to change as individuals grow older.

The main general feature of this evolutionary change seems to be that we probably rely on the same cognitive apparatuses for cooperating with cultural kin as those that had initially evolved to make us cooperate with genetic kin. In other words, cultural replicators in this case rely on genetic replicators to generate the relevant cognitive tools, and then "hijack" them for their own use³⁵. Put another way, the cognitive apparatuses involved in genetic cooperation get co-opted for cultural cooperation, which can itself be actualised across various levels of organisation (interactors at successively higher levels)³⁶. The anecdotal evidence supporting this claim consists of the ways in which humans have expressed their emotional drives that make us direct our cooperation towards cultural kin and higher-level interactors; these seem to be almost identical to the ways we express our emotional drives behind our cooperation towards our genetic kin, the most notable of which is perhaps "love" for one's country or countrymen. Empirical support for this claim can plausibly be found in fields such as sociology, anthropology, and literary studies.

Before turning to the third question which was outlined in the first paragraph of this section, it is worth pointing out the fact that the evolutionary process just described—the co-option of cognitive mechanisms originally meant for actualising genetic kin selection for the purpose of cultural kin selection—is actually one of the necessary conditions for the possibility of higher-level interactors evolving at all. To see why this is the case, recall that higher-level interactors in the sociocultural domain are generated mainly by cultural rather than genetic replicators. In order for the cultural replicators generating such interactors to spread through the population, they need to be able to direct the cooperative behaviours of lower-level cultural interactors towards themselves. Without the existence of the aforementioned genetically-produced cognitive apparatuses of humans, they would not have been able to start the process of doing so. Once they did start the process, however, there didn't seem to be any bounds to the vertical extent (number of successively higher levels) of the interactors that they could then produce.

³⁵ This is not to say that the interests of the cultural replicators and those of the biological replicators are necessarily at odds. What it is actually meant to convey is that they may be at odds or indeed aligned, as has already been discussed. Nonetheless, cultural replicators themselves don't seem to be capable of generating the necessary "hardware" for this task, though they certainly are capable of producing the relevant "software".

³⁶ This evolutionary process can appropriately be dubbed an exaptation, and I think the use of this term is advisable here because it makes clear the fact that it has something important in common with exaptation in biological evolution, namely that an adaptive trait becomes co-opted to perform a new function.

Let us now turn to the other two questions, namely that of the developmental question of how individual humans learn to fit into their distinct roles in societies and actualise the extent of the division of labour in their respective societies; and the evolutionary question of if, and how, division of labour at a social level has evolved in human cultures. I will now attempt to provide an answer which, once again, the answers will be brief and general, and aimed at only capturing the most essential features of the processes. I will begin with the evolutionary question.

Near the end of chapter one, I mentioned a class of higher-level adaptations that could count as individuating mechanisms only in the broad sense. This was because these adaptations didn't deal with conflict resolution directly, but were nonetheless relevant to individuation through their role in the integration of the higher-level unit and the increase in the interdependence of lower-level units. Moreover, I mentioned their status as instances of non-reproductive division of labour. It is worth pointing out that this is division of labour at a complex level, barely comparable to that seen in cyanobacteria with two kinds of cells, each doing a separate job. I also mentioned that they become more relevant during the later stages of the transitions. To bring an example, consider the evolution of organs and organ systems in the evolution of animals. Surely, the evolution of division of labour in animals must have started out with the lower-level units—the cells—diversifying and specialising in a developmental process in each generation. As the transition progressed, i.e. as larger, more complex animals evolved and occupied novel niches in increasingly complex ecological communities, two things happened in parallel. One was an increase in the number of cell types, the other new ways the cells of different types were organised together (McShea, 2001). For an instance, compare the exclusively intracellular digestion seen in sponges with the extracellular (as well as intracellular) digestion in the Eumetazoa; the specialisation of nerve cells, muscle cells and dermal cells and the subsequent formation of nervous, muscular or dermal organs (such as nerve cords, myotomes, and skins); or the evolution of eyes following the specialisation of light-sensitive cells.

Is a similar pattern observed in the case of sociocultural transitions? In other words, does division of labour increase in complex, two- (or perhaps multiple-) step processes as sociocultural transitions progress? To find the answer, the best place to look is most likely the field of economics, where the idea of division of labour first arose, and has been explored extensively. Once again, I can only use anecdotal evidence seems to try and support my claim that the answer

is an affirmative one: the modern world certainly houses much more complexity in terms of division of labour than did the pre-modern world; there are countless more roles an individual (or indeed any higher-level interactor) can fill in the tremendously large societies of today's world. Moreover, the evolutionary process does seem to be a two-step one, during the first of which relatively small societies see labour being divided among the individuals comprising them; while larger societies employ divide their labour among organisations, which consist of groups of individuals with well-defined roles³⁷.

The developmental question regarding division of labour can also be illuminated using biological analogy. Consider the case of eusocial insect colonies, or “superorganisms”. In such colonies, individual insects generally start out as more or less identical (unless of course the fact that some are male and some are female—the focus here is on the females). However, by the time they reach maturity³⁸, they will have developed into various castes, each suited to a different function, depending on the species. The way this happens seems to be a combination of genetic and, more importantly, dietary differences (Alexander, Noonan & Crespi, 1991). The diets of individual insects are decided and delivered to them by other individuals in the colony. Thus, division of labour is attained by a combination of genetic and non-genetic developmental factors and processes.

The case of humans is quite similar, though in an important way different as well. We begin our lives with a few instincts and an array of predispositions, as well as a massive capacity for learning things. We certainly do not start out knowing all the things we need to know in order to be able to conduct ourselves as capable individuals in a highly social and competitive setting. For that purpose, we start with learning from our family members, and later peers. Formal education is the next step in the process (which has not always been an option throughout human history; it may itself be regarded as an adaptive feature of our societies). Doubtlessly, genetic predispositions also play an important role in which humans will be better at which roles; thereby the development of humans into capable individuals and thus the actualisation of division of labour in human societies

³⁷ Although there is perhaps one important difference between organisations as such and organs and organ systems in the biological world: organs and organ systems cannot be interactors, while organisations are supposedly well capable of being so.

³⁸ What is meant by maturity here is not sexual maturity, as most individual insects in eusocial colonies are sterile. Maturity here is meant as reaching the final stage of their life cycle—passing the pupal stage in eusocial hymenoptera and undergoing the final moult in termites.

also relies on a combination of genetic and non-genetic factors. The main difference is that human societies rely on a plethora of cultural information for the purpose of the relevant learning, which is non-existent (or at least virtually absent) in all biological cases. An important similarity is that in both cases change in specialisation becomes harder as development progresses.

The non-nested hierarchical structure of human societies.

A notable difference between the hierarchical structure of interactors in the sociocultural sphere and that of those in the biological sphere is that biological interactors have strictly non-overlapping hierarchical structures, whereas the same cannot be said about interactors in the sociocultural domain. Some authors have argued that this might preclude the application of the multilevel selection framework to the social domain (McShea, personal communication). It is not clear why this should be true. Okasha (2006) suggests that strictly nested hierarchies are not a necessary condition for multilevel selection to occur in a population in response to a problem that arises when trying to define higher-level units of selection in terms of interacting groups of lower-level units. The problem is, in basic terms, that interactions among lower-level units are not necessarily transitive, and therefore need not produce strictly nested hierarchies, which is problematic because the biological hierarchy is typically represented as strictly nested.

An interesting question then would be to ask why biological hierarchies tend to be nested. A good place to look for a clue is instances where the interactions are in fact intransitive, and the higher-level units therefore overlapping. This happens mainly when the interactions are not very well-interrelated, which is exactly when there is little selection at the higher level. Such circumstances obtain when the potential transition to individuality at the higher level has not progressed very far. This explains why the well-definedness of the higher level unit and the interrelatedness of the interactions between lower-level units seem to present a chicken-and-egg problem: in an ETI, the two are interdependent and increase gradually. The take-away is that biological hierarchies tend to become more strictly nested as transitions progress. This means that the answer to the original question must have something to do with how transitions work.

I think the relevant difference between nested and non-nested hierarchies is that the former are more conducive to the alignment of the fitnesses of lower-level units than are the latter. This follows from the sharing of fates that results from being situated in better-defined groups. In other words, nested hierarchies limit the chances of lower-level units increasing their own fitnesses by

defecting from the higher-level unit and joining another³⁹. Transitions cannot progress very far if the lower-level units are not tightly bounded together, and nested hierarchies do exactly that. That is therefore why biological hierarchies tend to be nested. Also note that this is in fact a stronger version of the notion that hierarchical structures evolve as a response to conflict between the constituent units. To see why this is true, just recall that hierarchies emerge as a direct result of the evolution of individuating mechanisms (especially demarcating mechanisms), which are in turn mechanisms of conflict resolution. In other words, hierarchies are a way of making the boundaries between groups of interacting units clearer, and nested hierarchies are simply a further step in that direction.

Now that it's established that strict nesting is not necessary for transitions, we can turn to asking why it seems to be the case that human social interactors are more prone to having non-nested hierarchies. Why is it the case that business firms, for example, can easily span across states? Or that individuals can be parts of different organisations at the same time, while simultaneously belonging to families that are not part of any organisation? Answering this question comes down to finding out how stable units at higher levels can evolve while the lower-level units are still not tightly bound together; or in other words, how the conflict of interest arising from the lack of strict nesting does not disrupt the stability of the higher-level units. At this point, I do not have an answer to this set of questions. More theoretical advances in modelling, as well as looking more deeply into the differences between sociocultural and biological interactors is perhaps needed to find out why strict nesting seems to be a more crucial condition for the evolution of higher-level units in one domain than the other.

Internal selection and optimality.

So far, the implication of the application of the multilevel selection framework to the sociocultural domain seems to have been that in order for the higher-level units in a transition to function properly, selection at the lower level should be curbed entirely. This implication seems to follow from the fact that higher-level selection requires the alignment of interests among lower-level units and between the lower-level units and the higher-level units. I will argue that only the latter, and not the former, is the condition that needs to be satisfied. In other words, as long as the interests

³⁹ One illuminating example is the evolution of mutualism and parasitism. A parasite will most likely evolve into a mutualist if it cannot be transmitted horizontally (see Maynard Smith and Szathmáry, 1995).

of the lower-level units are aligned with those of the higher-level units, it does not matter if there is selection among them, as this selection only follows from conflicts of interest among lower-level units themselves.

Consider a biological example. In vertebrate development, some organ systems form through a selective process whereby cells which have a higher fitness within the context of the developing organism end up comprising the developed organism. The nervous system, for example, starts out by producing a much larger number of neurons than will be found in the organism at the end; a large proportion of these neurons die out, the survivors being those that have been better at receiving developmental signals (Wolpert, Tickle, & Arias, 2015). A similar process occurs in the development of the immune system, where cell lineages that react to “self” molecules die out. Nonetheless, in spite of the obtaining of the conditions for natural selection in the aforementioned examples, some authors have argued that these cases do not comprise genuine selection, since the cell lineages have no reproductive future of their own (See Godfrey-Smith, 2009). It is not clear why this should be relevant at all: as long as the conditions for natural selection obtain, the process is selective by definition⁴⁰.

Similar cases can be found in sociocultural evolution. I will attempt to bring a small number of such examples only, only sufficient to demonstrate the point. Consider, for example, firms within economies, academics in universities, soldiers in military units, and even office workers in bureaucracies. In each of these situations, the component units compete amongst themselves presumably due to conflicts of interests between them. However, it does not follow from this conflict of interests that the interests of the lower-level units should also be at odds with those of the higher-level units⁴¹. Therefore, selection at the lower level should not hamper selection at the higher level so long as it doesn't entail antagonism between units at the two levels. A more general conclusion is perhaps that this kind of “internal” competition would not be eliminated as long as

⁴⁰ For all we know, all life that has evolved on Earth will come to an end in a few billion years due to the Sun's inflation (unless of course some of it manages to make it to another planet). That certainly doesn't mean that natural selection has not been at work.

⁴¹ Note that this assumes a non-linear relation between the interests of the units at the different levels. In other words, if the fitnesses of the higher-level units were linear aggregations of those of the lower-level units, conflict of interest at the lower level would entail that at the higher level.

its benefits outweigh its costs. To see what costs and benefits these might result in, let us go back to our examples, both the biological and the sociocultural.

In the developmental cases mentioned above, the competition that takes place between cells results in fitness benefits for the organism, as well as costs. In both cases, the costs are obviously a considerable amount of energy and materials spent on producing cells which end up dying. The benefits differ slightly between the cases, but have something important in common: in the case of the development of the nervous system, the final nervous system will be one which is efficient at signal transduction; in the case of the immune system, the result is a system that responds strongly to foreign molecules, but (ideally—autoimmune diseases are far from rare) doesn't attack the organism itself. Both enhance the viability of the organism.

In each of the cases from the sociocultural domain, the situation is similar. The costs mainly have to do with the spending of resources in a suboptimal way, the benefits have to do with the end result for the higher-level units. In an open market economy, firms get the chance to compete, whereas in a state-run economy, such competition becomes less pronounced. This competition can in turn result in a better resource acquisition and production for the economy as a whole. The other examples have a similar structure. Bear in mind, however, that the exact costs and benefits and whether or not they outweigh each other depends on the specific ecological conditions and selective pressures present in the scenario (in a poorly supplied army, for example, it's probably best for the soldiers not to spend their limited energy on fighting amongst themselves).

This line of thinking can extend quite far, though I can only make suggestions in this regard here. For instance, consider the fact that competition for resources within an economy entails a degree of inequality, and the only plausible wealth-redistributing factor is taxation by the state, which in turn has an antagonistic effect on the competition that would increase the production of wealth in the first place. Political freedom is a closely linked matter, at the very least because individuals and firms are less able to pursue their economic goals within states where political freedom is limited. This in turn ties in with issues surrounding the nature of egalitarianism, collectivism, individualism, democracy, etc. The crucial point that links all these to the thesis of this paper is that they can all be seen as way in which the fitness interests of interactors could be aligned or at odds, and how they play it out. I think it's important to point out that the alignment or conflict of interests by itself cannot predict what will happen in situations where there are various interactors

with their own interests; some interactors might be more capable of working towards their interests than others, at the expense of others. One way to characterise this difference is by alluding to the notion of power, defined in terms of the relative capability of interactors in working towards their fitness interests. A powerful head of state, for example, may make use of resources to their own benefit at the expense of the lower classes, which may or may not be good for the society as a whole. In other words, power relations can be thought of as the way in which conflicting fitness interest can fight it out.

Now, given that the rate of cultural evolution is much slower than that of biological evolution, we come across an interesting question regarding the “optimal” relative selectability between individuals and higher-level units. What I mean by an optimality in this sense is basically a point at which higher-level units can function properly in spite of the restrictions this might put on individual freedom. To see why this has anything to do with the comparative rates of cultural versus biological evolution, notice that the costs of restrictions on individual freedom stem from the assumption that individual humans will not function efficiently if they feel too restricted⁴² due to their relatively fixed psychological dispositions. This is of course not to say that these dispositions are very rigid; surely there is a degree of flexibility involved. Nonetheless, the overall change in human psychology towards higher cooperativeness due to selection at higher levels is most likely much slower than the rate at which increasingly higher levels can evolve. It would be an interesting query into how this constraint, namely the individualistic disposition of humans does not preclude the evolution of successively higher levels, which ties in with the question posed in the section on the non-nestedness of the hierarchical structures in sociocultural evolution. My intuition is that it could have something to do with certain structural adaptations that make us individuals “feel” autonomous even though we might not necessarily be so. This could in turn tie in with the notion of “internal” competition; as long as competition between us individuals is not at odds with higher-level fitness, the successively higher levels can evolve with no hindrance. Nonetheless, a much more careful analysis is needed to provide satisfactory answers to such questions. My hope is simply that thinking of them in this framework would indeed be a step in the right direction.

⁴² The opposite is perhaps also true: situations where humans feel too isolated.

4. Motives and implications

“Are we stalled?”

In his 2007 paper “Are we stalled part way through a major evolutionary transition from individual to group?” Stephen Stearns makes an attempt at the applicability of the transitions framework to human evolution. As the title suggests, he poses the question of whether a similar process to the one in biological transitions has been working in human evolution, both genetic and cultural. Furthermore, he asks the question of whether the transition has been stalled midway. I think that in order to provide a satisfying answer to the question, we must first consider two important things.

The first is that the distinction between biological and cultural transitions, as well as their interrelation, should be explicit and clear: while cultural evolution can produce levels upon levels of hierarchical organisation, the much slower biological evolution may not be able to keep up, therefore resulting in conflict among individual humans with a strong desire for autonomy and higher-level units that would be better off if that autonomy was curbed. The second point is that much alike biological transitions, there is no reason to think that any transition must progress all the way forwards to total individuality at the higher level. A transition will progress only so far as external selective pressures allow it to do so; the phylogenetic tree abounds with individuals and groups that have advanced to various degrees in various transitions, and have stayed where they are for very long periods of time. The trend towards hierarchical complexity, so to speak, is a passive one that results from fixed lower bounds and virtually non-existent upper bounds.

There is no telling whether or not we as a species will progress towards higher-level units either culturally or biologically, since the exact selective pressures driving our cultural and biological evolution are not perfectly clear. However, one thing is certain: both our biological and cultural evolution have led us to higher levels of hierarchical complexity, the former in the past few million years, the former in the last two epochs, especially the current one (the Holocene). In the past ten thousand years or so, we have experienced increasingly large higher-level interactors, ranging from tribal confederations, villages, city-states, kingdoms, empires, nations states, and last but not least, large groups of cooperating nations such as the European Union, the Commonwealth, or the United Nations. Bear in mind that interactors need not be cohesive units, they can be relatively loosely organised. Through a transition, these loosely organised higher-level replicators *become* cohesive units. As such, the UN, for example, might someday become one such unit. Whether or

not this will actually happen will have to do with selective pressures, which are quite hard to predict. Nonetheless, it is certainly a possibility.

A possible Popperian objection

The thesis presented in this paper faces a possible Popperian objection, which is that it doesn't seem to be easily falsifiable. It's not easy to see how we could show that human societies don't have a hierarchical structure. The other side of the same coin is that hierarchical structures can relatively easily be "seen" in the human social world. In other words, is this thesis picking out something "real" about the way some things are, or imposing itself onto things? One possible response is that since hierarchical organisation entails the presence of individuating mechanisms, the thesis actually predicts their presence. This takes a step towards solving the problem, but the same problem holds to some degree: individuating mechanisms might also be imposed, rather than picked out, especially as they are multiply realisable (which means that many things can potentially be identified as individuating mechanisms).

The solution to the problem lies in acknowledging that the thesis in fact *isn't* and indeed *shouldn't* be easily falsifiable. As mentioned before, the thesis of this paper is highly abstract, and the point of having a highly abstract and general theory is often to bring a relatively large number of other, more falsifiable theories, under a large meta-theoretical umbrella. With the help of these less abstract and general theories, a vast number of phenomena can then be explained. In effect, the defence for the theory of natural selection as a unifying meta-theory also holds for the less inclusive multilevel selection theory; although to a lesser extent which is proportional to the lesser inclusiveness of multilevel selection theory. What follows is that the application of multilevel selection theory to sociocultural evolution should be only slightly more falsifiable than the application of the theory of natural selection itself to sociocultural evolution⁴³.

My aim of presenting this thesis has precisely been taking this very same step: to make a slightly stronger claim than the applicability of the theory of natural selection to sociocultural evolution which deals with *how*, in slightly less general terms, the theory of natural selection applies here. My specific claim has been that multilevel selection theory applies to sociocultural evolution. In

⁴³ A rather uninvited consequence of this is that this thesis is vulnerable to any serious objection to the weaker thesis of the applicability of natural selection to sociocultural evolution.

doing so, I have chosen a subset of the explananda of the theory of natural selection in sociocultural evolution as the set of explananda for the thesis.

The slightly less general theories that attempt to link the main thesis to even less general and more falsifiable theories take up most of the third chapter. The broadness of the thesis itself results in these theories to span a great variety of subject matters, ranging from anthropology to economics, and from political to moral philosophy. The theories in these subject matters in turn explain the concrete facts of the actual world. In this way, a hierarchy of theories is formed (perhaps it should be called a meta-hierarchy)⁴⁴ that links concrete facts, through a successively more general series of generalisations, to the thesis of this paper, and ultimately to the theory of natural selection itself.

It is indeed hard to see if there could be any theory more general than natural selection that could be applied to the sociocultural domain. In making this remark, I follow other authors who have argued that if any one theory is going to unify the social sciences, it must be the theory of natural selection. Following from the argument just presented, the thesis presented here is thus one further step towards the much desired unification of the social sciences. My hope is that this thesis does so by making a slightly stronger claim than the applicability of the theory of natural selection to sociocultural evolution, thereby eliciting more interesting questions that will attempt to link the concrete to the abstract and thus finding out whether the application of the theory of natural selection to the domain is in fact a good unificatory move in the sense that it will help us better understand the phenomena in the domain under one theoretical framework.

This is merely a repetition of the application of firstly the theory of natural selection and secondly multilevel selection theory to biology. These have most certainly been highly successful moves, to the extent that it's now perfectly sensible to claim that "nothing in biology makes sense except in the light of evolution" (Dobzhansky, 1973). Given the similarity of the respective sets of phenomena studied under the umbrella terms biological sciences and social sciences in very abstract and yet perhaps very important terms, namely that they both involve highly complex entities that undergo some sort of evolution, it is also sensible to think that the same is true for the latter set. To conclude, my hope is that the viewpoint presented here can bring such disparate

⁴⁴ The hierarchy is almost certainly non-nested: there are many phenomena that are the explananda of more than just one subject matter.

phenomena as has been mentioned and their relations to each other, under a single theoretical framework where they make sense "in the light of evolution".

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