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Steps to individuality in biology and culture

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Did human culture arise through an evolutionary transition in individuality (ETI)? To address this question, we examine the steps of biological ETIs to see how they could apply to the evolution of human culture. For concreteness, we illustrate the ETI stages using a well-studied example, the evolution of multicellularity in the volvocine algae. We then consider how those stages could apply to a cultural transition involving integrated groups of cultural traditions and the hominins that create and transmit traditions. We focus primarily on the early Pleistocene and examine hominin carnivory and the cultural change from Oldowan to Acheulean technology. We use *Pan* behaviour as an outgroup comparison. We summarize the important similarities and differences we find between ETI stages in the biological and cultural realms. As we are not cultural anthropologists, we may overlook or be mistaken in the processes we associate with each step. We hope that by clearly describing these steps to individuality and illustrating them with cultural principles and processes, other researchers may build upon our initial exercise. Our analysis supports the hypothesis that human culture has undergone an ETI beginning with a *Pan*-like ancestor, continuing during the Pleistocene, and culminating in modern human culture.

This article is part of the theme issue 'Human socio-cultural evolution in light of evolutionary transitions'.

1. Introduction

The major questions of this theme issue communicated to the contributors were (i) what are the critical stages in a major transition and (ii) is human society undergoing a major evolutionary transition into a social organism [1]. As 'major evolutionary transitions' have been interpreted in a variety of ways [2], we interpret these thematic questions about evolutionary transitions in terms of evolutionary transitions in *individuality* or ETIs. ETIs constitute a natural kind [3] as they involve similar assumptions, processes and outcomes [2,4–8]. We use the similar stages that ETIs proceed through in this paper as a lens to investigate individuality transitions in human culture. We approach the thematic questions above by first reviewing the critical stages or steps in the evolution of individuality in biology. We use the evolution of multicellularity in the volvocine algae as a model system to explain these steps to individuality. We then ask for each of these steps whether similar processes may be occurring in culture. As we are not cultural anthropologists, we may be mistaken in the processes we associate with each step, or we may miss aspects of culture that fit into the various stages. Our hope is that by describing and illustrating these steps to individuality, other researchers more familiar with human culture may improve upon our initial exercise.

There is interest in whether the social groups being created in today's culture through computer-assisted technologies constitute a new kind of evolutionary individual. We believe that to understand whether new ETIs are occurring, we must better understand the possible ETI that created humans in the first place. Did an ETI occur in the evolution of humans and their culture? That is the question we try to answer here and that is our interpretation of question (ii) by the organizers given above. Nevertheless, the approach taken here of applying ETI stages to study tool use in *Pan* and in hominins during the Oldowan and Acheulean time periods could be applied to human society today to ask whether additional ETIs may be occurring.

In evolutionary biology, the unit of selection and adaptation is the evolutionary individual. The evolutionary individual has changed dozens of times during the history of life on earth because of ETIs. During an ETI, groups of previously existing individuals evolve into a new kind of individual. Repeated ETIs have given rise to one of life's most familiar properties: its hierarchical organization. Examples of ETIs include the transition from groups of replicating RNA molecules (or genes) to networks of cooperating genes in a cellular genome, the transition from groups of bacterial and archaeal cells to the eukaryotic cell and the transition from unicellular to multicellular organisms. Although each of these transitions involves special considerations, the general steps of each ETI are similar, which is why ETIs are thought to constitute a natural kind. These steps are group formation, cooperation, conflict and conflict mediation, division of labour, decoupling of fitness between levels and heritability of the group phenotype [4,7,9]. Following a brief review of individuality, we address each of these steps in turn for both the volvocine algae and human culture.

2. Individuality

(a) Overview

What are evolutionary individuals? Can evolutionary individuals be identified in culture? In this section we address these questions. We introduce evolutionary individuality, give an example of an ETI (the evolution of multicellularity in the volvocine algae) and consider whether evolutionary individuals exist in the cultural realm.

All fields of science must define and characterize their most basic units. In evolutionary biology, the unit of selection and adaptation is the evolutionary individual. Multiple criteria, including indivisibility and heritable variation in fitness, have been used to identify evolutionary individuals (reviewed in [8], pp. 1–5). There is a large literature devoted to understanding biological individuality, with several collections of papers providing an overview of this exciting field [10–13].

New kinds of individuals have arisen during the history of life during evolutionary transitions in individuality (ETIs). During these rare events, groups of previous individuals evolved into new kinds of individuals, a process that has given rise to the hierarchical organization of life in which biological complexity is organized as a nested hierarchy. Hypercycles of replicating molecules evolved into genomes and simple cells, groups of prokaryotic (bacteria and archaea) cells evolved into eukaryotic cells, groups of unicellular organisms evolved into multicellular organisms and groups of multicellular organisms evolved into eusocial insect societies.

Some ETIs have occurred multiple times (as is seen in the evolution of multicellularity) while other ETIs have occurred only once (as is seen in the evolution of eukaryotes). ETIs are relatively rare evolutionary events, having occurred just dozens of times during the history of life on earth. As already mentioned, ETIs share common stages and processes: group formation cooperation, conflict, conflict mediation, division of labour, the export of fitness to the group level and the heritability of group traits.

While ETIs can differ in the nature of their interacting units, they proceed through similar stages leading to the evolution of a new kind of individual. The mechanisms underlying the evolution of multicellularity have been well studied, but, for other ETIs, the mechanisms are still being worked out. Nevertheless, even if the underlying mechanisms have not been determined in detail, the general aspects of the steps to individuality can be discussed and compared between biology and culture. Because the stages of an ETI are independent of the details of the mechanisms involved, we think the approach taken here of comparing stages between ETIs in biology and culture could prove useful. We do not need to understand the details of the mechanisms of cultural evolution to ask whether an ETI in human culture has occurred.

(b) Individuality in biology and the evolution of multicellularity

The evolution of multicellularity is one of the best-studied ETIs and the stages and mechanisms of this transition are relatively well understood. We focus on this transition when describing the stages in an ETI and when asking how these stages could fit with cultural evolution. We are using multicellularity as an example of an ETI because it is well understood and not because we think that the evolution of multicellularity is more similar to a cultural ETI than other biological ETIs.

During the evolution of multicellularity, the dominant level of selection transitions from that of the cell to that of an integrated group of cells, the multicellular organism. The evolution of multicellularity occurs when the unit of selection transitions from single cells to integrated groups of cells: multicellular organisms. Multicellularity has evolved dozens of times across the tree of life, including in animals, fungi, land plants, red algae, green algae and bacteria [14].

The volvocine green algae have been used as a model system to understand this transition [7,8,15–20]. The volvocine algae are a clade of freshwater, flagellated Chlorophycean green algae that span a range of complexity. There are unicellular species such as *Chlamydomonas reinhardtii*, undifferentiated multicellular species such as *Gonium pectorale* and *Pandorina morum*, facultatively soma-differentiated *Eudorina elegans*, obligately differentiated species such as *Pleodorina starrii*, and germ-soma differentiated species, including *Volvox carteri* (figure 1). An advantage of this lineage is that some of the extant intermediate species and forms are predicted to be similar to the ancestral forms during the ETIs in this lineage [18]. We will use this clade to illustrate the stages of an ETI and then as a lens with which to view possible evolutionary transitions in individuality in culture.

(c) Individuality in culture

Solitary cells are the initial individuals in the evolution of multicellularity. What are the initial individuals in the evolution of culture, that is, the individuals that are presumed to have existed before a possible ETI begins? We see two possibilities: single cultural traditions and the hominids whose behaviour expresses these traditions. Traditions are units of culture that are expressed through human behaviour and transmitted socially [22,23]. Cultural selection on traditions involves their persistence and transmission, just as natural selection on hominins involves their survival and

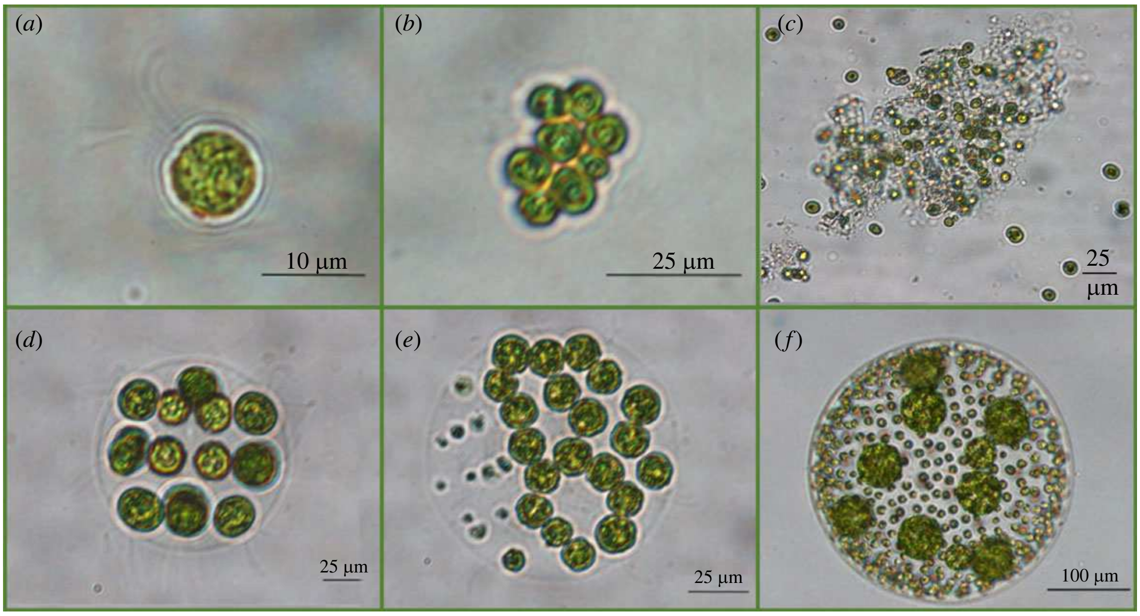

Figure 1. Examples of volvocine algae diversity. Panels (*a–c*) show *Chlamydomonas reinhardtii* in unicellular form in (*a*), after forming a group by staying together after division in response to the environmental stress in (*b*), and after forming a disorganized group via aggregation in response to environment stress (*c*). Panel (*d*) shows the undifferentiated *Eudorina elegans*, panel (*e*) shows the soma-differentiated *Pleodorina starrii* and panel (*f*) shows the germ-soma differentiated *Volvox carteri*. Figure modified from [21]. (Online version in colour.)

reproduction (the two basic components of an individual's fitness in biology).

ETIs begin with groups of individuals. We consider groups of hominids (mainly hominins but also *Pan* as an outgroup for comparison, as discussed below) with their traditions from two perspectives: (i) groups of traditions whose dynamics are shaped by hominins and (ii) groups of hominins whose interactions are affected by traditions. While both perspectives illustrate the interplay between biology and culture, we focus on interactions among traditions in the first perspective and interactions among hominins in the second.

As we go through the exercise of applying ETI stages to culture, we consider both groups of traditions (whose dynamics are mediated by humans) and hominins (whose behaviour both creates and is affected by cultural traditions). We focus predominantly on traditions involved in large game carnivory during the Oldowan and Acheulean, an activity that persisted across time periods that involves multiple traditions and hominins. We also touch upon features of modern human culture that are relevant to this potential transition.

The nature of an evolutionary transition implies a starting point that must be assumed or characterized as the beginning point for the transition. In biology, phylogenetic methods and outgroup comparisons are used for this purpose. In our analysis of the evolution of human culture, and the possibility of an ETI there, we use *Pan* (chimpanzees and bonobos) as the outgroup. This is discussed in more detail below as we proceed through the stages in an ETI.

Our analysis based on ETI stages is parallel to but consistent with the rich literature of gene–culture coevolution and cultural group selection. Extensive work has gone into understanding how interactions between genes and culture have shaped human evolution [24–28]. Multi-level selection has been employed to understand the importance and dynamics of selection acting on cultural groups; a field termed cultural group selection. Cultural group selection proposes that between-group differences in culture have been subject to selection [29–32].

(d) Oldowan and Acheulean carnivory and tool use

When discussing culture and hominins, we consider carnivory (including large game hunting) and tool manufacturing and use during a specific time period: the end of the period of Oldowan culture and technology and the rise of the Acheulean culture and technology. This occurs during the Pleistocene; the Oldowan period occurred between approximately 2.6 and 1.6 million years ago and Acheulean technology first appeared approximately 1.7 million years ago [33]. Oldowan technology has been primarily found at African sites and consists of simple stone tools with flakes removed, resulting in a sharpened edge [34]. Such tools were used to process carcasses, as shown by the butchery marks on the bones of prey [35–39], and they may have also been used to obtain and process plant food, including underground plant storage organs, and modify nonedible plant tissues [40–42].

While Oldowan technology consisted of simple stone tools, the Acheulean technology that replaced it was more complex and consisted of more refined handaxes with two sharpened sides as well as flakes of stone that were used for other purposes such as the processing of plant material for consumption and the creation of non-stone tools [43,44]. Acheulean technology has been found in Africa, Europe and Asia. Handaxes may have been involved in animal butchery [45–47]. Multiple other tools were created during this time, including flakes and bone tools that could have been used for digging [48].

There were several hominin species present during the Oldowan period that could have used Oldowan technology. *Homo habilis* and *Australopithecus* (*Paranthropus*) *boisei* remains have both been associated with Oldowan tools in Olduvai Gorge, Tanzania. In Gona, Ethiopia, *Homo erectus* crania and *Australopithecus garhi* remains [49,50] have also been found near Oldowan technology. While remains of two *Australopithecus* species have been found in association with Oldowan technology, researchers disagree on whether these smaller-brained species manufactured Oldowan tools [40]. Early Acheulean technology spread as species such as *H. erectus* dispersed across continents, bringing tool-making with them. The spread of Oldowan and then Acheulean technology occurred during a period of high hominin diversity. [51]

We focus on this time period for several reasons. The Oldowan is one of the first times hominins were known to manufacture stone tools and marks the first appearance of well-preserved culture in the fossil record [52]; moreover, the addition of meat into the hominin diet may have led to a number of biological adaptations and behavioural and cultural changes (reviewed in [39]). The Oldowan is therefore a key milestone in human evolution, but the subsequent invention and spread of the more complex Acheulean represents a technological shift that occurred during an important period in human evolution.

3. Group formation and group size

(a) Overview

The first step in an ETI is the formation of groups. This can occur in two different ways: through informationally distinct and different units coming together (as is seen in symbiosis), or through identical units staying together after reproduction (as in seen in many forms of multicellular development). Group formation through unlike units coming together occurs with hypercycles [53,54] and eukaryogenesis [55,56] and gives rise to egalitarian transitions [57,58], in which the group members are initially distinct and different. By contrast, fraternal transitions [57] involve groups that form through individuals staying together after reproduction. Fraternal groups tend to be informationally identical (barring mutation) and their fitness interests are more aligned initially because of the high degree of genetic relatedness.

Group size can vary in biological ETIs, ranging from groups of only two members (seen in the evolution of the eukaryotic cell) to trillions of members (seen in some multicellular organisms). We now compare group formation, group size and regulation of group size during the evolution of multicellularity with similar issues in cultural evolution.

(b) Group formation in the volvocine algae

The formation of cell groups is the first step in the evolution of multicellularity and can be examined in the volvocine green algae. The unicellular *C. reinhardtii* forms groups in response to environmental stress (figure 1*b*,*c*), including predation and high salinity [59–62]. These groups may be formed through two pathways: coming together (aggregative multicellularity) and staying together (products of cell division do not separate). For example, cells aggregate in groups in response to environmental stress; these aggregates are held together by excreted extracellular matrix and can contain up to thousands of cells (figure 1*c*) [21,63,64]. Since colonies form via aggregation and cells can join or leave the group, the colony boundaries are not well-defined when compared to those of obligately multicellular species such as *Volvox* (figure 1*f*). *Chlamydomonas reinhardtii* can also form clonally developing groups in response to stressors such as the presence of predators (figure 1*b*). These groups develop when daughter cells fail to separate after division [61].

Group formation and larger group size may provide protection against predators that would otherwise consume single cells. The groups that form in response to stressors, including predation, can be too large for predators such as rotifers to consume [60]. These predators preferentially eat the unicellular organisms that are not members of groups, demonstrating the selective benefits associated with being in a group. In *Chlamydomonas*, the size of facultative groups is not under genetic control. Facultative groups of cells can range in size from four cells to thousands of disorganized cells (figure 1*b*, *c*) [64], with genetically identical populations producing a wide range of group sizes (D Davison 2021, personal observation). While group formation in *Chlamydomonas* is facultative, groups always develop in other volvocine algae species. This development occurs when a cell divides and the daughter cells stay together. Since all the cells in a multicellular volvocine algae colony with obligate multicellularity are genetically identical, the evolution of multicellularity in the volvocine algae is an example of a fraternal transition.

The regulation of group size (body size) in obligately multicellular volvocine algae species is under genetic control. Genes necessary for obligate group formation in the volvocine green algae have been identified. The *RB* gene, an important cell-cycle regulator, likely played a key role in the evolution of obligate group formation. The transformation of the *RB* gene taken from a multicellular species into the primarily unicellular *Chlamydomonas* is sufficient for the formation of obligately multicellular groups in the transformed *Chlamydomonas*, showing that group formation is under genetic control [65]. Other genes are also involved in the regulation of group formation and group size, including the cyclin gene family, which expanded during the evolution of multicellularity and is part of the same cell cycle regulation pathway as *RB* [65,66].

(c) Group formation in culture

As discussed previously, we start with two different kinds of individuals during the evolution of human culture: cultural variants termed traditions and the hominins that create and transmit these cultural variants. Consequently, group formation may refer to hominin groups, groups of traditions, or groups of hominins along with their traditions. We consider both groups of traditions (whose dynamics are created by hominins) and groups of hominins (whose interactions are affected by cultural traditions).

To help illustrate what a group of traditions is, we focus on the example introduced above of carnivory in the Oldowan and Acheulean, discussing a limited number of core elements of this system [37,67]. We will also use this example in later sections as we progress through the ETI stages. Carnivory, including big game hunting, involves obtaining raw materials, producing tools, obtaining carcasses and then processing the carcasses [37]. In order for the final step—the processing of carcasses—to occur, the other traditions must also take place. Some traditions in this group cannot exist without the other traditions. For example, carcasses cannot be processed without first being obtained, and tools cannot be produced without raw material. Because of the co-occurrence of these traditions, which together make up a larger cultural practice of carnivory, the traditions can be considered part of a tradition group [68].

During the Oldowan, group-living hominins carried out the traditions described above as part of their foraging behaviour. Hominins identified and selected rocks to be turned into tools and other rocks to use in flaking. They then obtained carcasses using methods that likely varied across sites and may have included ambush hunting, short chases and scavenging [39,42]. The tools they made earlier were then used in carcass processing, and hominins may have occasionally transported these tools over several kilometres [42] to the location of the carcasses.

Before the Pleistocene (during the Pliocene), hominins may have formed multi-male, multi-female groups with either female dispersal (with related males staying with their natal group, as is seen in chimpanzees) or bi-sexual dispersal [69–71]. Due to the limited evidence available, our understanding of Pleistocene hominin group size and structure is still preliminary. However, it's possible that kinship relationships may have played an important role in group formation and the structuring of social relationships, including interactions centred around obtaining and processing food [72]. Groups may not have been based around nuclear pair-bonded families; instead, kinship relationships may have been recognized and could have played a role in structuring social relationships, including interactions surrounding obtaining and processing food [73,74]. Group sizes for individuals using hominin technology have been estimated to be between 18 and 28 individuals, with members of these groups potentially interacting in larger social networks [74]. As group size estimates from other evidence and other locations have produced estimates of group sizes ranging between 15 and 23 individuals [75], it is possible that group size was at least partially regulated, although the mechanisms by which this could occur are unclear.

Early Acheulean technology is typically associated with *H. erectus*. This species had a larger brain relative to previous *Homo* species and may have had a more complex social life with more sophisticated systems of communication and information transfer. The size of hominin groups could have increased during this period [76], with larger groups facilitating the successful dispersal of *H. erectus* out of Africa [77]. Consequently, the shift from Oldowan to Acheulean culture may have also been associated with changes in the structure of biological groups of hominins and expanding hominin group size. That said, the structure of Pleistocene hominin groups is not well-supported by empirical evidence.

When studying evolutionary transitions, it is informative to have an outgroup that likely possesses some of the characteristics that may have been seen at the start of the transition. In the evolution of multicellularity in the volvocine algae, that outgroup is the unicellular *Chlamydomonas* (figure 1*a*); in the case of human culture, we turn to *Pan* (chimpanzees and bonobos), the closest extant relatives of humans. While we discuss cultural traditions in *Pan*, we recognize that the question of whether non-human animals have culture is contentious [78–85]. What is relevant to including *Pan* in our analysis is not whether *Pan* has human-like culture but whether *Pan* has some of the antecedents of human culture such as individual traditions and can therefore function as an outgroup in our analysis.

We start by considering how multiple traditions can be integrated into groups. This can be examined in *Pan*, where the formation of groups of traditions occurs when several traditions, each of which can be modified, become part of a more complex behaviour. Traditions in *Pan* vary between groups, suggesting that cultural traditions may be stably inherited [83]. We can examine group formation in *Pan* traditions by examining the use of tools to extract food from structures such as termite mounds. Termite fishing is a tradition that can vary between chimpanzee communities, with different tools (such as leaf ribs or non-leaf materials) used to extract termites [84]. Therefore, termite fishing is an example of a tradition that has two different variants. It can be transmitted between chimpanzees via social learning and persists over time. In other words, *Pan* has traditions and cultural selection could act on these traditions.

The termite fishing tradition can exist on its own or be implemented in conjunction with a tradition involving the use of other tools to open a termite mound. This small group of two traditions involves the use of strong tools to open a food site such as a termite mound followed using more delicate tools to extract the termites [86]. Traditions involved in the use of blunt force to obtain food (such as the use of rocks to crack nuts [87,88] are also part of the cultural repertoire of many chimpanzees. The incorporation of a second tradition that is used along with the first, where both traditions are part of the same larger behaviour, illustrates how a simple group of *Pan* cultural traditions may form when multiple traditions come together. In this way, one can see how aspects of the first step of an ETI in culture is taking place in *Pan*.

A key aspect of group formation and evolution is group size. While the organization of multiple traditions into groups is present in both chimpanzees and humans, group size varies dramatically between the two. In chimpanzees, the number of traditions integrated into the same group of traditions is limited relative to the cultural complexity seen in humans [86]. Human cultural traditions may form quite large integrated systems; it is not clear whether these groups of traditions even have an upper size limit.

Groups of traditions in human culture appear to lack the regulation of group size seen in biological ETIs. With regard to the regulation of group size, groups of modern human traditions have more in common with the aggregative groups of thousands of *Chlamydomonas* cells (figure 1*c*) than to the highly regulated groups of cells that make up obligately multicellular species such as *Volvox* (figure 1*f*). On the other hand, large groups of human traditions are notable for their integration, something that is absent in the large groups of *Chlamydomonas* cells shown in figure 1*c*. In any event, while the formation of simple groups of chimpanzee traditions is similar to small groups of *Chlamydomonas* cells that can form via aggregation, the large complex groups of traditions characteristic of modern human culture appear to be quite different from biological ETIs in that groups of traditions appear to be lacking strictly regulated group numbers and group sizes.

4. Cooperation

(a) Overview

Group living facilitates the evolution of cooperative interactions among individuals in the group. Cooperation among group members occurs when members of a group benefit from working together. In biology, cooperation is thought to evolve through three (sometimes overlapping) pathways: reciprocity, multi-level selection and kin selection. Once it evolves, cooperation sets the stage for conflict, the evolution of conflict mediation and further cooperation that make up the subsequent stages of an ETI. Over time, groups of cooperating individuals may become so integrated that the group becomes a new kind of individual. Our overview of cooperation follows references [56,89,90] (see tables 17.1 and 17.2).

Cooperation can take multiple forms and have different kinds of benefits, depending on the nature of the interactions and the individuals involved. The benefits can be of the same kind or different kinds. For example, the cells in a multicellular organism with only one cell type will contribute the same type of benefits, while the cells in a multicellular organism with different types of cells may contribute different kinds of benefits to the group. The costs and benefits of cooperation to the group can be additive (such as sharing a piece of food) or synergistic (such as feeding on each other's waste products). Synergistic cooperation occurs when the benefits and costs of cooperation are shaped by the strategies of interacting partners in a nonlinear fashion. It can be difficult to cheat with synergistic forms of cooperation.

The type of cooperation and the benefits derived from this cooperation affect subsequent ETI stages. If cooperation is costly to the cooperating individuals, cheaters who do not pay those costs may have higher fitness. This can lead to the evolution of conflict and conflict mediation. There are other ways in which group living can lead to conflict, especially if cooperation is based on enforcement, or if the groups are based on exploitative interactions to begin with. For example, exploitative interactions like predation or parasitism have been hypothesized for the origin of mitochondria in the evolution of the eukaryotic cell (reviewed in [91]). Biological groups need to obtain resources for component individuals in a concentrated local space and get waste products out. In general, group living leads to conflicts of numerous types and these conflicts must be mediated for cooperation to evolve. We discuss conflict and conflict mediation stages in the next section.

(b) Cooperation in the volvocine algae

As the cells in a volvocine algae colony are genetically related, cooperation in this lineage primarily evolved through kin selection and multi-level selection acting on cells and groups of cells. There are multiple ways in which cooperation among cells in a volvocine algae colony occur. For example, cooperation occurs via flagellar action that gives rise to colony motility. For the colony to swim efficiently, cells must beat their flagella in a coordinated fashion. However, there are costs associated with having flagella for any given cell, as the cell cannot divide or cannot divide as quickly when flagella are present. As a result, a cell with a mutation that allows it to divide rapidly rather than contributing to colony motility may outcompete cells without such mutations within the group, even though this mutation is costly to the group. Another form of cooperation is seen in the shared extracellular matrix (ECM) (the clear matrix surrounding the cells, seen in figure 1*d–f*). Most multicellular volvocine algae species have a shared ECM, which is made of glycoproteins that are secreted by individual cells [92]. An expansion of the ECM and associated gene families occurred during the evolution of multicellularity in this lineage [66]. The ECM is a shared resource that each cell expends resources to contribute to; as a result, defection could be selected for [18] by way of not producing ECM and investing those resources elsewhere (including in reproduction).

There is also cooperation in the sense of integration between specialized cell types in a *Volvox* colony. Germ cells (the larger cells in figure 1*f*) specialize in reproduction and somatic cells (the smaller cells in figure 1*e,f*) specialize in viability functions like motility. As discussed in more detail below in §6 below, these specialized cells would do poorly outside of the group, but together in a group constitute a good team and can bring high fitness to the group. Mutations in the genes underlying the somatic cell phenotype produce unregulated cell division and cancer-like phenomena in algae colonies [93,94].

There are two different ways in which cooperation occurs. These are seen in our discussion of the volvocine algae and we will return to them when discussing cooperation in cultural evolution. The first way is a part-based notion of cooperation or collaboration among parts or members of an integrated group; the second way is an individual-based notion of cooperation among evolutionary individuals. A unicell that shares resources with other cells in a population is cooperating with another evolutionary individual. However, when a cell is part of a multicellular organism, it cooperates with other specialized cells to increase the fitness of the organism that they are a part of.

In multicellularity, these two meanings of cooperation have to do with which level is the individual, the cell or the multicellular organism. If the cooperating cell is the individual, cooperation exists in the first individual-based sense. If the cooperating cell is part of a higher-level individual (the multicellular organism), cooperation exists in the second part-based sense. The part-based sense overlaps with the idea of division of labour and integration, discussed in more detail in later sections.

(c) Cooperation in culture

Cooperation in human culture can also involve both part-based and individual-based notions. If hominins are evolutionary individuals, then food-sharing among members of a social group is an example of an individual-based notion of cooperation. When traditions are integrated into a larger unit they are cooperating in a part-based sense, as the traditions are part of a larger cultural unit. The benefits of this cooperation may be synergistic, with traditions that are part of a larger unit contributing different benefits to the group. Traditions may benefit from cooperation when they co-occur and interact with other traditions in such a way that causes the humans that possess them to better survive and reproduce or better transmit the traditions.

Cooperation among traditions is present in the hominin carnivory exhibited by Pleistocene hominins. Hunting requires obtaining raw material for making tools, producing those tools, using tools to hunt, and then using additional tools to process carcasses [68]. This behaviour involves the expression of an integrated set of cultural traditions, some of which may have limited benefit to humans outside of the context of the other traditions. As a result, single traditions that are part of a tradition group may be unlikely to persist or be transmitted by hominins outside of the context of other traditions. For example, traditions surrounding the production of tools are unlikely to arise without the existence of traditions involved in obtaining materials to make the tools.

Oldowan hominins engaged in cooperative foraging and food sharing [95]. Meat was likely a shared resource, and hominins may have cooperated by sharing meat. Such food sharing may have included providing food for reproductive females in the group [40]. Moreover, cooperation via the exchange of information on how to make Oldowan tools could have occurred. Oldowan technology is present at multiple different sites across a large region and time period, and multiple different species may have been creating and using the same technology [96]. This raises the possibility that the knowledge of how to make the stone tools may have been transmitted socially both between groups of the same species and between species. Cooperation may have therefore been present between groups of hominins, not just within groups. Such a view is consistent with smaller hominin groups forming larger meta-populations of interacting individuals [74] in which multi-level selection could potentially occur. That said, it is possible that the widespread distribution of Oldowan tools is due to a combination of individual learning and low-fidelity social learning, rather than due to high-fidelity social learning [80].

It is unclear whether patterns of cooperation changed during the Acheulean. However, the ETI framework suggests the hypothesis that cooperation among both traditions and hominins increased during this time. While many of the species that used Oldowan technology had smaller brains and it is not clear if they engaged in complex cooperative behaviour, *Homo erectus* had evolved by approximately 1.89 mya and was characterized by having larger brain and body sizes. *H. erectus* may have engaged in food sharing, with reciprocity and the provisioning of young potentially both playing important roles [71,95]. *H. erectus*, whose brain sizes were larger than what was seen in previous hominins, could have been born in a relatively undeveloped state that required greater cooperation and caregiving among adults to ensure offspring survival. A higher level of cooperation may have allowed *H. erectus* to alter their behaviour in response to their environment and to persist at a time when other hominins went extinct [97]. As these connections are based on limited data, more research is needed to understand the evolution of cooperation during this time period.

We end by comparing cooperation among Pleistocene hominin traditions and modern human traditions to the cooperation seen among chimpanzee traditions. Modern human culture is characterized by large systems of integrated traditions. This stands in contrast to early Pleistocene cultural systems, as Oldowan carnivory likely involved a relatively limited number of traditions [98]. Chimpanzee culture is not characterized by large systems of integrated traditions. That said, there are some cultural behaviours that involve the incorporation of a limited number of traditions, reminiscent of what may have occurred during the Oldowan [98]. For instance, the termite fishing tradition can be combined with another tradition involving the use of strong tools to force open termite nests [99]. While these traditions persist and can be transmitted alone, in some groups the two have been incorporated into a group of cultural behaviours. This indicates that there could be a degree of cooperation among some chimpanzee traditions, but it is limited relative to hominins in terms of the number of traditions involved, their reliance on each other for continued persistence and transmission, and their degree of integration. The observed difference between cooperation in the human cultural realm and cooperation in the chimpanzee cultural realm suggests that the ETI stage of cooperation is far more developed in hominins than in the *Pan* outgroup and has likely evolved in the human lineage.

5. Conflict and conflict mediation

(a) Overview

As seen in the volvocine algae examples above, the evolution of cooperation sets the stage for cheating and conflict. When the fitness interests of the members of a group are not aligned, conflict evolves, and members of the group pursue their own fitness interests, often at a cost to the entire group. Defectors can take advantage of the common resources created by the cooperators or can quickly reproduce in a way that destabilizes the group, as is seen with cancerous cells in multicellular organisms. Groups can evolve into new kinds of individuals only if conflict mediation mechanisms evolve that reduce conflict between group members and minimize the chances of within-group change [4]. Developmental processes evolve to minimize conflict in the cell group and increase the heritability of group-level phenotypes [100]. These conflict mediation mechanisms, also termed ‘individuating properties’ [101], take different forms across systems and ETIs.

(b) Conflict and conflict mediation in the volvocine algae

There are multiple mechanisms that mediate conflict among cells in the volvocine algae. Perhaps the most important one is the evolution of a single-celled bottleneck stage from which multicellular colonies develop [102,103]. Since all cells in a multicellular colony develop from that single-celled bottleneck, high levels of relatedness align their fitness interests and kin selection operates more effectively [104,105]. Moreover, when all cells develop from a single cell, genetic variation among cells in minimized, thereby limiting the potential for selection among cells to operate [106].

The evolution of genetic control of cell number and group size also mediates conflict in the volvocine algae [107]. Developmental processes limit the maximum number of cells in a colony [108,109]. This may can mediate conflict as it reduces the benefits of defection, since cells that conserve resources (for example, by not investing in shared ECM) cannot use those resources to increase their own reproductive output [18,19]. Mechanisms controlling cell number are likely to be selectively favoured because cell-level cheating and over-replication can have harmful consequences for the group. Across volvocine species, increasing group size comes with costs that would be incurred if unregulated cell division occurs. The primary cost of larger group size is getting resources into a concentrated group of cells and waste products out. For larger algae groups, there is also the cost of increased drag through the water column. In larger multicellular volvocine species, this cost is offset by greater investment in motility in the form of somatic cells that are specialized in motility and colony survival [110]. There are other selective benefits associated with larger group size. As group size increases, the reproductive potential also increases, predators specialized in the consumption of smaller organisms can be avoided, and cells can specialize in different functions of the group [7]. These costs and benefits have resulted in group size being shaped by selection.

Increasing group size sets the stage for conflict, particularly if group size is unregulated so that there is an advantage to rapidly dividing cells [107]. This conflict is due to the cell-level benefits that occur when cells invest in their own replication at a cost to the group. If a cell has a mutation that causes it to go through many additional rounds of division and give rise to many more offspring cells than the other cells in the colony, its direct fitness will increase because of this enhanced representation in the group. However, reproductive mutants that invest heavily in reproduction would not be able to invest in survival and motility due to trade-offs between flagellar motility and cell division. Cells that cheat by dividing in an unregulated fashion could therefore cause the fitness of other cells in the colony to decrease. Genetic control of cell number and the genetic regulation of group size inhibit such conflict.

(c) Conflict and conflict mediation in culture

Conflict and conflict mediation in culture can be studied from two different perspectives: conflict among traditions, whose dynamics are shaped by hominins, and conflict among hominins, whose interactions are affected by their cultural traditions. We begin by highlighting how conflict and conflict mediation may occur among traditions, discussing both large game carnivory and sets of human cultural traditions more generally.

In the evolution of multicellularity in the volvocine green algae, development from a single-celled bottleneck increases genetic relatedness and reduces the potential for conflict among group members. However, human cultural traditions do not exhibit such information homogeneity. Instead, it appears that groups of traditions are composed of separate traditions that have different informational content. In this sense, ETIs in the cultural realm are more like egalitarian transitions than fraternal transitions. Cycles of cooperation, conflict and conflict mediation may be different in egalitarian transitions (such as the evolution of eukaryotes) from in fraternal transitions. For this reason, we may expect to see differences between our multicellularity example of a biological ETI and a possible cultural ETI.

The synergistic nature of cooperation among traditions is likely to affect their subsequent conflict and conflict mediation. Cooperation during hominin large game carnivory involves co-occurrence of multiple traditions that are functionally dependent on each other. For instance, carcass processing is dependent upon first obtaining carcasses. In general, existing traditions may increase or decrease the probability that new traditions are added to a cultural system and can also modify the likelihood that existing traditions will be maintained in a system [111].

A high degree of interdependence raises questions regarding the extent to which the fitness interests (in terms of persistence and transmission) of independent traditions may by aligned by the way of how they are added to the group. Cultural traditions are created and modified by humans and the creation of this variation can be intentional or random [112,113]; when intentional, the process is fundamentally different from random mutations that generate variation in biological evolution [114,115]. How does the process by which cultural variation is created affect the types of interactions that occur between traditions? Does the process by which new traditions arise and are added to groups of traditions reduce the potential for conflict between component traditions? How interdependent must traditions be for their interests to be aligned, and to what extent do these functional dependencies reduce conflict?

Modern human culture is filled with conflict-mediating mechanisms, such as rules, regulations, norms and laws with associated punishments, along with feedback loops that enforce these conflict mediators. These cultural mechanisms of conflict mediation serve to inhibit cheating and other forms of conflict among humans. Such enforcement facilitates the continued cooperation and collaboration of the group. While many are similar to the kinds of conflict mediation mechanisms seen in biology, it is not clear whether the evolution of these conflict mediators in human culture followed the selection dynamics seen in cycles of cooperation, conflict and conflict mediation in biology.

Conflict among individual humans likely occurred in the early Pleistocene but widespread warfare was not present [116]. Evidence of conflict is seen in a 1.77 million year old *Homo* cranium, which bears evidence of head injuries that are likely the result of interpersonal violence or accidental injury [117]. Given that aggression is common among primates [118], it is probable that conflict among hominins included instances of interpersonal aggression. How this conflict was mediated and cooperation promoted in the social groups that existed at that time is presently unclear.

In *Pan*, the number of traditions in a group of traditions is limited and the traditions are not as interdependent as they are in humans. Due to this lower degree of integration, groups of *Pan* traditions are expected to be more prone to being disrupted by lower-level, that is tradition-level, selection.

6. Division of labour and fitness decoupling between levels

(a) Overview

High fitness requires success at both reproduction and survival. However, there is usually a trade-off between these two fitness components, such that high effort at one fitness component usually detracts from the other. Reproductive division of labour occurs when group members specialize on the fitness components of the group: survival or reproduction. Reproductive division of labour is a key step in an ETI and is fundamental to individuality, so much so that it is a criterion used to identify evolutionary individuals [8,106,119].

Division of labour is evolutionarily important because of its effects on fitness at the cell level and at the group level. During ETIs, as members of the group specialize in one of the two basic fitness components, they would lose their overall fitness were they to try to live outside of the group. Members specialized at reproduction could not survive outside of the group. Likewise, for members specialized at survival, they cannot reproduce if they are not a part of the group. While having low fitness overall, these reciprocally specialized members may constitute a good team when in a group and bring high fitness to the group [120].

Fitness decoupling refers to the high fitness of the group even as its members would have low fitness were they to exist outside of the group [16]. Another way of describing fitness decoupling is to observe that fitness has been exported from the lower level (cells) to the higher level (multicellular organism).

(b) Division of labour and fitness decoupling in the volvocine algae

Differentiated volvocine algae species such as *Volvox* (figure 1*f*) have reproductive division of labour as they possess specialized germ and somatic cells [121]. Germ cells (the larger cells in figure 1*f*) are specialized in reproduction while somatic cells (the smaller cells in figures 1*e*,*f*) do not reproduce and instead specialize in survival by increasing colony motility and allowing colonies to continue swimming while undergoing cell division [110]. Flagellar beating also serves to increase transport of resources into the group and waste products out of the group. Since somatic cells cannot reproduce, their fitness is dependent upon the fitness of the group, and potential conflict between cells is mediated. Moreover, the specialized germ line reduces the per-generation mutation rate [106,122,123], which reduces the potential for selection to act at the lower level by decreasing genetic variation among cells. The evolution of reproductive division of labour precedes the evolution of other forms of cell specialization [124], indicating that regulating reproduction in a group is a necessary first step before other forms of cell–cell cooperation, including new cell types, can evolve.

In the volvocine algae, reproductive division of labour plays a key role in decoupling group fitness from cell fitness. The cessation of reproduction, which is seen in somatic cells (the smaller cells in figures 1*e*,*f*), is costly at the cell level but beneficial to the group. The fitness of the group is no longer the average of cell-level fitnesses, since cell-level fitnesses are decreased, but instead group fitness emerges from interactions between cells. This change in the relationship between cell-level fitness and group-level fitness is central to the decoupling of fitness and emerges from reproductive division of labour.

(c) Division of labour and fitness decoupling in culture

What form does cultural division of labour take? Does fitness decoupling occur in culture? During ETIs, division of labour specifically refers to specialization in the components of fitness such as reproduction and survival. Consequently, to address these questions, we first need to describe the fitness components of cultural selection. In the biological realm, the two main components of fitness are survival and reproduction, with overall fitness often taken as a product of these two components that trade-off with one another. Consequently, high overall fitness requires a balance between survival and reproduction. The biological fitness of hominins is also studied in these terms.

The analogues to survival and reproduction for cultural traditions are, respectively, persistence and transmission. It is not clear to us whether traditions within larger groups of traditions (including large game hunting) specialize on persistence and/or transmission. Traditions in a group may contribute different benefits to the group and these benefits may affect the transmission and persistence of both the traditions and the group. However, traditions in a group might not be specialized on contributing to the persistence and/or transmission of the group. As a result, reproductive division of labour and fitness decoupling may not exist among traditions as it does among cells in multicellular groups.

Although reproductive division of labour (specialization on transmission and/or persistence) on may not exist in culture, division of labour more generally is implicit in our discussion of tradition groups in hominin culture. General division of labour refers to sets of cultural traditions in which component traditions differ in their tasks and contribution to an overall goal. While reproductive division of labour may not exist among the traditions that make up a large game hunting system, there still are likely trade-offs between the functions of traditions. Hunting large game in *Homo* is an example of such a goal and provides examples of division of labour in a group of traditions. As described previously, traditions regarding obtaining and processing tools and meat must all be present and expressed through the behaviour of hominins for a hunt to be completed successfully. Each of these traditions is part of the larger system of traditions and many component traditions only make sense in the context of the other components of that system [125,126].

Additionally, when stone tools were used for multiple purposes, trade-offs between functions could have occurred. For example, Oldowan tools were likely used for multiple purposes, including processing meat and obtaining plant material. Could a lack of specialization have inhibited the effectiveness of these tools for any given task? If trade-offs existed, could they have been resolved with the advent of more sophisticated Acheulean technology? The answers to these questions remain unknown and additional research is needed to understand the importance of trade-offs in stone tools.

Despite a lack of clear reproductive division of labour among traditions, fitness decoupling may still occur in the cultural realm for some groups of traditions. This is the flip side of the synergistic nature of the cooperation among traditions in a tradition group. When alone, such traditions may have little cultural fitness. Traditions such as toolmaking could be less likely to persist or be transmitted outside of the context of the other traditions in the group. This may occur because toolmaking is dependent upon the prior collection of raw materials and is most beneficial to humans when it is followed by the use of those tools to obtain and/or process carcasses. Since some traditions are likely to have lower or no fitness outside the group context but their presence in the group increases the fitness of the whole group because of the interactions between group members, it is possible that the fitness of those traditions has been exported from the tradition level to the group level.

Do reproductive division of labour and the export of fitness occur among hominins in hominin groups? While a degree of reproductive division of labour could occur in some situations, it seems different from the obligate reproductive division of labour seen in the evolution of multicellularity and in the other biological ETIs, including eusocial insect societies in which reproductive and non-reproductive casts exist. Moreover, while group-living animals (including hominins) may experience decreased fitness if they leave the group, this is not sufficient to say that fitness decoupling has occurred. Fitness decoupling depends on the synergistic nature of the cooperation in the group and the prospects for fitness outside of the group. We therefore see the possibility of a different pattern emerging when we examine groups of traditions (whose interactions are mediated by humans) as opposed to groups of humans (whose interactions are affected by traditions).

By contrast, there is probably a lower level of functional integration and fitness decoupling in chimpanzee culture. While *Pan* groups vary in the groups of traditions they possess [83], many of these traditions may not be integrated into a single, larger cultural system. Many *Pan* traditions function alone, and their expression does not depend on the presence or absence of other traditions. That said, there is some evidence of division of labour in multi-step tool use systems, in which tools must be obtained and occasionally modified prior to their use [83,86]. However, these systems only contain a limited number of traditions and the component traditions can exist on their own, unlike many of the traditions seen in modern human culture. In the light of these considerations, we conclude that the fitness decoupling stage of ETIs is likely not occurring in *Pan*, but could be occurring in hominins although not based on reproductive division of labour like it is in multicellularity.

7. Heritability of the group phenotype

(a) Overview

Increased heritability of the group phenotype is the final step in an ETI. Natural selection requires heritable variation in fitness, so when the group phenotype is heritable, selection can act on the group as a whole [127]. The heritability of group-level traits is related to the evolution of conflict-mediating mechanisms, division of labour and export of fitness previously discussed. Increased heritability occurs following the evolution of division of labour because specialized germ cells develop into colonies with both germ and somatic cells, and therefore the colony phenotype, not the cell phenotype, is inherited. With increased heritability of fitness at the higher level, the group evolves into a new kind of individual.

Group-level traits require special consideration because some group traits are just aggregative properties of lower-level traits while others emerge out of interactions among the lower-level units, cell–cell interaction in the case of multicellularity. Heritability of aggregative properties of the group depends primarily on cell division, however, heritability of group-level traits such as the reproductive division of labour requires development and the expression in time and space (within the developing group) of the traits underlying conflict mediation and other individuating mechanisms.

(b) Heritability in the volvocine algae

Multicellular volvocine algae colonies possess heritable phenotypic variation, which is necessary for selection to act on the cell-group level. Traits that are properties of the multicellular group evolve during the transition to multicellularity. These phenotypes range from aggregative group-level traits that are simple additive functions of cell-level traits, such as group size (in terms of numbers of cells), to emergent (non-aggregative) traits that are due to interactions between cells and developmental processes, such as the development of specialized cell types like reproductive and somatic cells [128]. In species such as *Volvox* (figure 1*e*), the phenotype of the differentiated group as a whole is inherited through the specialized germ cells, which themselves do not express the somatic phenotype present in the somatic cells of the next generation. By contrast, this is not the case in the disorganized groups of cells shown in figure 1*c*.

(c) Heritability in culture

Human cultural evolution can occur when new traditions arise or are modified, creating variation among traditions. The new or modified tradition may be transmitted via social learning and can then spread [129]. Single traditions may be selected for and spread independently of other traditions, or integrated sets of traditions may be transmitted among hominin groups. Traditions may spread because they contribute to increased genetic fitness of the humans expressing them, or they may spread because they have other properties that increase their likelihood of transmission and/or persistence. For example, the spread of Acheulean technology could be the result of hominins preferentially using and transmitting Acheulean technology, it could result from hominin groups that possess Acheulean technology outcompeting those without, or it could be a consequence of both processes acting in concert.

The transmission of human culture is notable in that it involves high-fidelity imitation or even over-imitation [130,131], which causes both traditions and groups of traditions to be inherited faithfully. Heritability is high and selection can act at the group level. As a result, cultural evolution can give rise to diverging lineages of traditions and sets of traditions. By contrast, *Pan* cultural transmission predominantly involves lower-fidelity emulation and there likely are not successive rounds of innovation that give rise to the substantial increases in the size of groups of traditions [85,129,132].

Biological heritability among hominins is separate from the heritability of cultural traditions. Heritability exists at the organism level, as hominins pass on their genes via sexual reproduction, and the traits their offspring possess are shaped by the genes received from both parents and developmental processes interacting with the environment. When two hominins reproduce, their genes will be passed on to their offspring following biological laws regardless of the cultural traditions they possess. However, the cultural environment can affect the development of the phenotype, including behavioural traits. In short, culture is an important component of the environment that hominins develop in and can therefore affect their phenotypes.

8. Discussion

(a) Comparing biological and cultural transitions

We reviewed the main steps of evolutionary transitions in individuality (ETIs) in biology and applied them to cultural evolution to understand whether and how a transition in individuality in human culture may have occurred. The main stages we considered are group formation (with increases in group size), cooperation, conflict and conflict mediation, division of labour and the export of fitness to the group level and the inheritance and heritability of group-level traits. We summarized these stages and used the volvocine algae to help explain how these stages occur in a biological ETI, the evolution of multicellularity. We then discussed how those stages may have occurred during an ETI in culture. We discussed two different but interacting and interdependent parts of culture: cultural traditions and the hominids whose behaviour underlies the traditions. For each stage, we considered both groups of cultural traditions that are underpinned by hominids, and the hominids whose fitness is affected by the cultural traditions they express.

Our analysis (summarized below in table 1) supports the hypothesis that an ETI occurred in human culture. The groups in this ETI comprise two kinds of individuals, which stands in contrast to biological transitions that typically involve groups of one kind of individual. For example, the evolution of multicellularity occurred when selection transitions from acting on single cells to acting on groups of cells, and the evolution of eukaryotes involved selection transitioning from acting on prokaryotic cells to groups of prokaryotic cells (an

Table 1. Similarities, differences, and areas for future research when comparing the ETI stages in chimpanzee culture, human culture and multicellularity.

Stage	Chimpanzee culture	Human culture	Multicellularity
Initial individuals	*Pan* traditions	Hominins and traditions	Cells
Boundaries	Relatively discrete	Boundaries need to be clarified	Clear boundaries in most cases
Group size	Small	Potentially unlimited in modern humans	Regulated in multicellular species
Cooperation	Cooperation occurs between chimpanzees. There is some degree of integration and other forms of cooperation between traditions	Cooperation occurs between humans. Cooperation occurs between traditions in the sense of collaboration and integration	Cooperation is present among cells in the multicellular organism, including the production of shared resources and reproductive altruism
Source of new variants	*Pan* innovation and random variation	Human innovation and random variation	Random mutation and recombination
Conflict and conflict mediation	There are examples of conflict mediation among chimpanzees but not among traditions in an integrated group of a small number of traditions	Numerous examples of conflict mediation mechanisms among modern humans. May be affected by human innovation of new traditions	Conflict and mechanisms of conflict mediation have been characterized
Cycles of cooperation, conflict and conflict mediation	Not clear how selection mechanics work	Not clear how selection mechanics work	Cycles exist and drive increased complexity
Trade-offs	Do persistence and transmission trade off?	Do persistence and transmission trade off? Other tradeoffs exist, as tools were likely used for multiple functions	Trade-off between survival and reproduction nearly universal in biology
'Reproductive' division of labour	Are there traditions that specialize in transmission or persistence?	Are there traditions that specialize in transmission or persistence?	Present in all individuals.
Fitness decoupling	Traditions have fitness outside of the group context	Tradition fitness likely lower outside of the context of the tradition group. Fitness of a tradition group not a simple average of tradition fitness	Cell fitness is lower if specialized cells leave the group; fitness of the group is not a simple average of cell fitness
Heritability	Most traditions are transmitted on their own with lower fidelity	Groups of cultural traditions are transmitted with high fidelity through social learning	The multicellular phenotype is vertically transmitted with high fidelity through reproduction
Complexity	Relatively low complexity	A range of complexity exists. Is the complexity organized hierarchically?	A range of complexity exists and is organized hierarchically

archaeal genome and a bacterial genome that are part of the same cell). The proposed cultural ETI is therefore different from previously described biological ETIs, despite potentially proceeding along similar stages. The cultural ETI involves groups of two kinds of individuals—hominins and integrated groups of cultural traditions—that merge into a new bio-cultural individual. This new individual combines not only two kinds of individuals but also the change from selection acting on single traditions to integrated groups of traditions. These tradition groups are created and transmitted by social hominins; the tradition groups, along with the social hominins, make up a new kind of bio-cultural individual.

By using biological ETIs as a lens through which to view potential cultural ETIs, we characterize how ETI stages could apply to these bio-cultural groups. We focus on the process by which an ETI occurs and find that there are both similarities as well as differences between the process of biological and cultural ETIs that require further research to understand ETIs in the cultural realm (table 1).

We have considered the early Pleistocene and Oldowan and Acheulean technology and tool use. As the stone tools that are characteristic of these periods are largely associated with carnivory, we discuss the traditions involved in a simplified system of large game hunting. The shift from the Oldowan to the Acheulean traditions likely involved both cultural selection acting on groups of traditions and biological selection acting on hominins. Cultural selection may have occurred if hominins that could use both types of cultural traditions and tools (such as *H. erectus*) preferentially used and transmitted Acheulean technology and the sets of cultural traditions needed to create it. Biological selection could have occurred if hominin survival was tied to the technology they used.

Modern human culture is notable for its complexity, which stands in contrast to the organization of culture in our outgroup species, chimpanzees and bonobos. In biology, ETIs may be used to understand how the increased levels of complexity inherent in the hierarchy of life evolves [133]. While cultural complexity has undoubtedly increased in the human lineage and groups of cultural traditions satisfy many of the criteria used to identify units of selection [68], further research is needed to identify whether these increases involve hierarchical complexity. It is not clear whether the complexity of human culture is hierarchically organized like it is in biology. Do analogues to the hierarchy of life exist in human culture?

Even in the biological realm, not all increases in complexity are due to ETIs and changes in nestedness, the level of hierarchical organization. Complexity can also increase when the number of parts and number of part types increases. For instance, the number of cells and cell types has increased in certain animal lineages. Such changes are not necessarily associated with changes in the unit of selection. Could a similar process—one that does not involve a transition in nestedness or hierarchical level—have played out during the evolution of complex culture?

In table 1 we summarize the similarities and differences we have found between culture and biology with regards to the steps involved in an ETI. When we compared the ETI stages in biology and culture, we found that several of the ETI stages, when applied to culture, appear to have key differences relative to biology. First, while both human and chimpanzee cultural traditions can exist in groups, there are important differences in group size and regulation of group size. In biological ETIs such as the evolution of multicellularity, group size—that is, body size—is genetically regulated and an upper bound is set in most species. In the volvocine algae, this upper bound ranges from four cells in *Tetrabaena* to thousands of cells in *Volvox* species. In chimpanzee culture, traditions that do not occur solely on their own can exist in tradition groups [86]. By contrast to both biology and *Pan*, the size of modern human cultural systems is large, growing, and it is unclear whether an upper bound even exists. It is equally unclear what processes govern which traditions are lost from expanding groups of cultural traditions, and where the boundaries of groups of large groups of modern human traditions lie.

It is unclear how similar cycles of cooperation and conflict among traditions are to the selection dynamics underlying the cooperation and conflict cycles we see in biological systems. The main way in which cooperation is present among traditions is that traditions are tightly integrated, interdependent, and work together as part of a larger unit. While we see conflict mediation mechanisms throughout human culture, further research needs to identify whether these mechanisms mediate conflict among traditions within the same group, between traditions in different groups, or between human beings within the group.

Evolutionary individuals are characterized in part by the existence of spatial and temporal boundaries [8]. While the boundaries of Oldowan and Acheulean carnivory could be characterized by delineating the boundaries of the humans involved, and the boundaries of, say, meat production in modern human culture could perhaps be roughly characterized, it may be harder to identify the spatial and temporal boundaries of more complex modern cultural systems, including religious systems that contain numerous traditions among widely dispersed human groups. Delineating the boundaries of cultural systems will help distinguish between these possibilities, as will a joint analysis of groups of human traditions with their underlying groups of humans. Although there is division of labour in the cultural realm in the sense that there are different traditions with distinct roles in the same group, there may not be reproductive altruism and reproductive division of labour in the sense of specialization in traits related to persistence and transmission of traditions. More research needs to be done on whether traditions within a group specialize on the cultural fitness components of persistence and transmission or whether there is a trade-off between the two fitness components.

Groups of traditions are so interwoven that some traditions are unlikely to be transmitted or persist outside of the context of the group. This suggests that the fitness of traditions is dependent upon the fitness of the group of traditions, which is consistent with groups of traditions being units of selection and evolutionary individuals. However, the relationship between the fitness of traditions and fitness of the tradition group requires more work. Finally, the fidelity of transmission varies between chimpanzee culture, human culture and multicellularity, with the high-fidelity transmission of human culture being more consistent with high-fidelity transmission in biology than the low-fidelity transmission seen in chimpanzee social learning. Chimpanzee and human culture are both transmitted through horizontal and vertical social learning, while information in biological ETIs is commonly transmitted vertically, although horizontal transmission does occur and can be quite important.

(b) What is the cultural evolutionary individual?

Every field of science must define its basic units. In evolutionary biology, that unit is the individual, the unit of selection and adaptation. In biology, we can study how new kinds of evolutionary individuals arise from groups of previously existing individuals via the stages in ETIs. We have applied these stages to cultural evolution to understand whether an ETI has occurred in the cultural realm. We considered two interdependent parts of culture: groups of cultural traditions and the social, interacting hominins that create and transmit the traditions. We found similarities and differences when applying the stages of an ETI to the evolution of groups of traditions.

The ETI framework has previously been applied to understanding the evolution of humans and their cultural traditions [68,134,135]. The approach taken here of comparing stages emphasizes the process of an ETI. In contrast, Davison *et al.* [68] focused on the individuality criteria characteristic of products of ETIs and concluded that these tradition groups met criteria characteristic of biological individuals. Integrated groups of human cultural traditions, as is seen in large game hunting, were found to satisfy many of the criteria used to identify biological individuals. These groups of traditions were found to have boundaries, informational uniqueness, be indivisible, possess putative group-level adaptations, and have division of labour among the component traditions

[68]. This suggests that groups of traditions are subjected to cultural selection [136] and that such groups could evolve into evolutionary individuals.

Culture is created and transmitted by humans and so we conclude that the groups of traditions along with the humans expressing the traditions may constitute a new kind of bio-cultural evolutionary individual. Selection may act on integrated units of biological hominins and groups of cultural traditions, which together may be a new kind of evolutionary individual. Further research will require delineating the boundaries of such an individual and characterizing the interactions between hominins and groups of traditions in an ETI framework.

Consistent with this possibility, coevolution between culture and genes is known to occur [24–26,137,138], and cultural group selection likely played a role in the evolution of cooperation among human beings (reviewed in [29,30]). Selection for groups of cultural traditions involved in the domestication, milking and milk processing of ungulates likely shaped the evolution of lactose tolerance in humans [26,28,138,139]. Similarly, the cultural traditions involved in language likely coevolved with culture, brain size, and the morphological changes necessary for speech [27]. The coevolution between genes and groups of cultural traditions is consistent with the possibility that rather than operating at the level of hominin groups or of groups of cultural traditions on their own, the new kind of evolutionary unit involved social hominins and groups of cultural traditions.

9. Conclusion

We have characterized the key stages of evolutionary transitions in individuality and discuss whether humans could be undergoing a transition in individuality. The key stages are group formation, cooperation, conflict and conflict mediation, division of labour and fitness decoupling between levels, and inheritance of group-level traits. We used the volvocine algae as a model to illustrate the steps to the evolution of individuality in biology. We then applied these steps to hominin culture. We focused on the evolution of groups of cultural traditions from single traditions and on the culturally mediated interactions of hominins that create and transmit these cultural traditions. We primarily discussed the early Pleistocene, a key period in human evolution in which a shift from one set of traditions (the Oldowan industry) to a new set of traditions (the Acheulean) was present. As evolutionary transitions require a starting point, we followed the use of outgroup analysis in biological transitions and used *Pan* as an outgroup for the evolutionary transition to individuality in human culture.

Our analysis (summarized in table 1) supports the hypothesis that human culture has undergone an evolutionary transition in individuality beginning with a *Pan*-like ancestor, continuing during the Pleistocene, and possibly culminating in modern human culture. The structure of groups of cultural traditions in hominins differs from what is seen in chimpanzees, our outgroup in this analysis. The transition from the Oldowan to the Acheulean cultural systems is consistent with selection acting on groups of cultural traditions, though a causal relationship cannot be inferred from the existing archaeological data. Moreover, the close relationship between hominins and groups of cultural traditions raises the possibility that together, they are a new kind of evolutionary individual.

However, while we found that cooperation, conflict and conflict mediation exist in human culture, there are differences that warrant further research. It is not clear whether there were cycles of selection dynamics involving cooperation and conflict during the evolution of culture, similar to what occurs during the evolution of multicellularity. It is also not clear whether cultural complexity is characterized by a nested, hierarchical organization as it is in biology. As our perspective as biologists may be limited, future research should focus on identifying such cycles as a possible pathway through which increasing cultural complexity could have arisen. Most importantly, more work needs to be done on the basic units of cultural evolution. Researchers should more fully characterize the individuals that could function as units of selection during an evolutionary transition in individuality.

Data accessibility. This article has no additional data.

Authors' contributions. D.R.D.: conceptualization, formal analysis, investigation, writing—original draft, writing—review and editing; R.E.M.: conceptualization, funding acquisition, investigation, supervision, writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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