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The cultural evolution of emergent group-level traits

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Abstract: Many of the most important properties of human groups – including properties that may give one group an evolutionary advantage over another – are properly defined only at the level of group organization. Yet at present, most work on the evolution of culture has focused solely on the transmission of individual-level traits. I propose a conceptual extension of the theory of cultural evolution, particularly related to the evolutionary competition between cultural groups. The key concept in this extension is the emergent group-level trait. This type of trait is characterized by the structured organization of differentiated individuals and constitutes a unit of selection that is qualitatively different from selection on groups as defined by traditional multilevel selection (MLS) theory. As a corollary, I argue that the traditional focus on cooperation as the defining feature of human societies has missed an essential feature of cooperative groups. Traditional models of cooperation assume that interacting with one cooperator is equivalent to interacting with any other. However, human groups involve differential roles, meaning that receiving aid from one individual is often preferred to receiving aid from another. In this target article, I discuss the emergence and evolution of group-level traits and the implications for the theory of cultural evolution, including ramifications for the evolution of human cooperation, technology, and cultural institutions, and for the equivalency of multilevel selection and inclusive fitness approaches.

Keywords: altruism; cooperation; cultural group selection; inclusive fitness; innovation; institutions; interdependence; multilevel selection; niche construction

1. Introduction

Humans are social animals, creatures of culture. Cultural traits are transmitted across generations, and varieties of socially learned norms and behaviors compete in a manner that is analogous to Darwinian natural selection. Over the last few decades, a theory of cultural evolution has arisen to describe the transmission of traits via social learning rather than genetic inheritance, as well as the ways in which genes and cultural traits coevolve (Boyd & Richerson 1985; Cavalli-Sforza & Feldman 1981; Durham 1991; Mesoudi 2011; Richerson & Boyd 2005; Whiten et al. 2011). Despite the claims of some who doubt the applicability of evolutionary models to cultural evolution (e.g., Claidière & André 2012; Fracchia & Lewontin 1999; Pinker 2012) and despite the real need for better, more explanatory models specific to cultural evolution (Mesoudi 2007; Sperber & Claidière 2006), an evolutionary theory of culture is here to stay. Cultural knowledge and behaviors are transmitted from generation to generation, and improved ideas and practices replace those that are less effective. Formal cultural evolutionary theory has gained additional robustness from models that show that natural selection can operate on cultural variants even if traits are not discrete and even if transmission is highly error-prone (Henrich et al. 2008).

The development of a cultural evolutionary theory, however, has suffered from an overemphasis on the experiences and behaviors of individuals at the expense of acknowledging complex group organization and behavior. For example, Richerson and Boyd (2005), two of the seminal figures in the development of a formal theory of cultural evolution, have defined culture as "information capable of affecting *individuals'* behavior that they acquire from other members of their species through teaching, imitation, and other forms of social transmission" (p. 5, italics

added). Cultures, however, are more than collections of individuals with shared traits. Cultural groups are organized, and organization matters. I argue that many important behaviors related to the success and function of human societies are only properly defined at the level of groups. I further argue that group-level traits, which involve organized collections of differentiated individuals, present a unit of cultural selection that is not encompassed by selection on individuals. This implies that selection on group-level traits is qualitatively different from selection on groups as defined by traditional multilevel selection (MLS) theory, which does not account for emergent traits based on group organization. A further implication is that a fully fleshed out multilevel selection theory of cultural evolution cannot be reduced to an inclusive fitness approach that focuses solely on the individual, as some have argued (see discussion in Pinker 2012).

In this target article, I will discuss the significance of what I term *group-level traits* in the context of human cultural evolution. I will first describe what I mean by group-level traits. Second, I will show that this type of organization is not fully accounted for by the multilevel selection perspective currently in vogue to describe evolutionary competition between cultural groups. Third, I will extend this analysis to show that *cooperation* is insufficient as the defining feature of humans groups and that in many contexts *collaborative interdependence* is more appropriate. Fourth, I will discuss how group-level traits emerge from collections of individual actors. Fifth, I will discuss mechanisms by which group-level traits are maintained, transmitted, and evolve. Sixth, I will argue that the interactional complexity of human societies supports extending the perspective of multilevel selection to incorporate the causal interactions between individuals and groups and that this extended perspective eliminates the equivalence between multilevel selection and inclusive fitness approaches to modeling evolution. Finally, I will

suggest directions for future research and theoretical development to better understand the evolution of group-level traits.

2. What are group-level traits?

Consider two armies squaring off. On one side we have the Barbarian Horde, a ragtag group of bloodthirsty killing machines. Each individual Barbarian is a deadly warrior, savage and merciless. Nevertheless, they have minimal group-level organization beyond attempting to avoid hurting one another – they are essentially an undifferentiated mass. On the other side is the Roman Legion. Individually, each Roman soldier is a skilled fighter, but would tend to lose in one-on-one combat with a Barbarian. The Romans, however, are a highly regimented unit. They have differentiated roles and hierarchical organization. Each soldier understands his role and how it relates to his fellow soldiers. In a fight between armies of equal size, the Romans will tend to dominate over the Barbarians, not because each Roman is better than each Barbarian, but because group-level organization allows the Romans to outmaneuver their opponents. Here I am using the terms "Roman" and "Barbarian" rhetorically rather than historically, but a dramatic historical example of this kind of confrontation is the famous Battle of Thermopylae in 480 BCE, in which a small but highly organized Greek force of about seven thousand men used a phalanx formation to successfully defend their front against Persian forces of more than 100,000 soldiers for a full week (before finally succumbing). The properties that allowed one group to triumph or persist against another in these cases did not belong to each individual group member, but rather emerged from the organized interactions between those individuals. I term such properties *group-level traits.*

Group-level traits are possible when individuals display both *differentiation* and *organization*. By differentiation, I mean that individuals take on different roles. The assignment

of these roles may be based on differences in innate physical characteristics or abilities, in age or extent of experience, or in deliberate training and specialization. By organization, I mean that differentiated individuals coordinate and collaborate for a shared purpose. Group-level traits rely on organization, but the organization itself is not the trait. Group-level traits are related, but not equivalent to institutions, which are "the laws, informal rules, and conventions that give durable structure to social interactions in a population" (Bowles 2004, p. 47). Instead, a group-level trait is the *phenotypic effect* of social organization. Thus, examples of group-level traits are the music rather than the rock band, the election of a leader who reflects the public interest rather than the democratic voting system, the sailing ship's voyage rather than the crew positions, the economic surplus rather than the market economy.

The significance of differentiation and organization is well known in evolutionary theory in the context of the major transition from single-celled organisms to multicellular life (Maynard Smith & Szathmary 1995; Michod 2007; Michod & Nedelcu 2003; Michod & Roze 1997; Okasha 2005). Indeed, there are a number of similarities in the distinction between individual cells and a whole organism and that between individual humans and emergent group organization. The somatic cells of a multicellular organism give up their right to reproduce without bound for the sake of propagating the germ cells that share their genomic sequence. Natural selection can act on individuals because the traits of the individual cells are subsumed into the larger organism; somatic cells cooperate with one another and inhibit the unbounded reproduction common to single-celled creatures (Michod & Roze 2001). Although they each share the same genetic code, the cells are differentiated by experience, chemical environment, and gene expression.

Somatic cells meet the criteria for Darwinian evolution – there is heritable variation that

influences fitness (Jablonka & Lamb 2005) – yet we do not usually think of the cells in the body as undergoing individual evolution (except perhaps in the case of cancer cells). Reproductive success for a multicellular organism translates not to the propagation of the traits of any one cell, but rather to the traits that emerge from the interconnection and cooperation among cells. A better-organized collection of cells is a fitter multicellular individual, and it is this organization that is selected for. Selection therefore operates on traits that involve the interactions of many individual cells. These traits do not exist within any individual cell, but only in their organized aggregation. It follows that if a heritable trait found in a group of multicellular individuals exists not as a property of each individual but as an emergent property of their organized interconnectedness, and if groups possessing this property increase their ability to propagate over groups without it, then selection will favor such groups.

Human groups organize in ways that produce emergent group-level traits. These traits produce between-group differences in genetic and cultural fitness and are heritable through cultural transmission. Group-level traits are not expressed by any single individual in the group, but emerge only from the structured organization of differentiated individuals. The reduction of culture and cultural practices to individual-level variants therefore misses an essential component of what enables human groups to succeed, as well as a key component in the evolution of cultures and societies.

2.1. What is a group?

To paraphrase Wilson (2002), a discussion of the role of group-level traits in evolution requires an unambiguous definition of groups. Yet groups may constitute quite different things at different times. The Roman Legion acts as a unit during battle, and the fate of each individual depends on the behavior and coordination of his brothers-in-arms. So the entire Legion is a group

exhibiting certain traits. Historically, however, soldiers in Roman battalions were drawn from many different cultural and ethnic populations, with diverse diets, languages, and customs. Off the battlefield, individuals organized into different group configurations, producing different types of traits. A deer hunter and a bowyer (bowmaker) might collaborate far from the fighting zone to their mutual benefit. Such a relationship, if largely uncomplicated by the actions of other individuals, would also constitute a group. Discussing the more traditional approach to multilevel selection theory, which deals with the selection of individual-level traits in a group context, Wilson writes: "When the trait is a social behavior, the fitness of an individual is determined by its own traits and the traits of the individuals with whom it interacts. These individuals constitute the group, which must be identified accurately to calculate the fitnesses that determine the outcome of evolution. It follows that groups must be defined separately for each and every trait." (Wilson 2002, p. 15). Group-level trait groups should be defined similarly. The trait-group, to use Wilson's (1975) term, is the collection of individuals interacting to produce the trait in question. A group may consist of a simple dyad or a population of thousands.

2.2. Not all collective behaviors are group-level traits

Collections of individuals can exhibit many behaviors that lone individuals cannot, but not all of these behaviors should be considered emergent group-level traits. For example, prey animals in large groups can use simple, individual-level rules to generate flocking, schooling, or herding behavior to more effectively find food or evade predators (Sumpter 2006). Collections of humans making independent evaluations can often make optimal decisions by averaging across all individual assessments (Surowiecki 2004). These kinds of collective behaviors are clearly important in the ecological behavior of humans and other species, and exert influence on evolution by creating new selection pressures (Lewontin 2000; Odling-Smee et al. 2003), yet are

qualitatively different from group-level traits. In contrast, Woolley and colleagues (2010) recently presented a series of experiments showing that the collective ability of a small group to solve problems (the group's collective intelligence) emerged from communication between the group members and was uncorrelated to the intelligence of the individuals in the group. Though the authors did not investigate exactly how the groups solved problems, other researchers have shown that groups in which individuals possess different abilities are often better able to solve collective problems (S.E. Page 2007; Post et al. 2009).

Wimsatt (1997, 2006) discusses properties of systems that are *aggregate*, rather than emergent, as having four qualities: (1) the system property is invariant to rearrangement of the parts, (2) the system is qualitatively similar under addition or subtraction of parts, (3) the system property is invariant to regrouping of the parts in system subgroups, and (4) there are no cooperative or inhibitory interactions among the parts of the system that affect this property. Many collective behaviors are largely aggregate, exhibiting qualities 1–3. They result from a number of interchangeable individuals acting independently (though they each react to different local stimuli) and tend to have qualitatively similar behavior for a wide range of group sizes. Flocking birds, for example, may inhibit or elicit cooperative behaviors in one another, but birds could be added or removed from the flock without qualitatively altering the collective behavior. Meanwhile, group-level traits are emergent to a much larger degree, because they depend strongly on specific arrangements of differentiated actors in specific organizational roles (and do not meet aggregate qualities 1–3). The difference between aggregate and emergent properties is often relative, but a useful heuristic for distinguishing group-level traits from collective behaviors is that the latter depend strongly on the specific organization of differentiated individuals, whereas the former do not.

3. Group-level traits and cultural group selection

Darwin (1871) originally proposed that, at least in the case of humans, many psychological traits related to empathy and altruism would have been selected against at the individual level and so must have evolved because groups of cooperative individuals would outperform selfish groups. Wynne-Edwards (1962) later developed a theory of group selection in which he proposed that predators should exhibit restraint in reproduction to avoid overexploiting their resources and that such restraint could evolve as a result of being group-beneficial. However, the logic of Wynne-Edwards' argument was rightly criticized (Williams 1966) as being incompatible with natural selection – less "prudent" predators would outcompete their more restrained neighbors.

If well-defined groups compete, however, and the variance of a trait tends to be higher between than within groups, then it is theoretically possible for an altruistic, group-beneficial trait to emerge, because groups with many individuals possessing such a trait will have higher mean fitness than groups with fewer altruists. This point is well supported by formal models (Henrich 2004a; Price 1972; Wilson 1975; Wilson & Dugatkin 1997) and has found empirical validation (Goodnight & Stevens 1997; Wade 1978). This newer group selection perspective, closer to Darwin's original ideas than to those of Wynne-Edwards, has since been adopted as the *multilevel selection* (MLS) framework (Bijma & Aanen 2010; Wade et al. 2010; Wilson 1997; Wilson & Sober 1994; Wilson & Wilson 2007).

Recently the MLS perspective has been applied to culturally transmitted traits in humans (Boyd & Richerson 1985; 2005; Henrich 2004a; Richerson & Boyd 1998; Soltis et al. 1995; van den Bergh & Gowdy 2009) under the heading *cultural group selection*. This perspective applies the same logic as MLS (and shall hereafter be referred to as cMLS) and works as follows. Altruists, who contribute to the average group fitness at a personal cost, are outperformed by

selfish individuals within groups, but altruistic groups outperform selfish groups. Therefore, if the variance within groups is sufficiently low and the variance between groups is sufficiently high, between-group selection can have a bigger influence than within-group selection, and selection for altruistic traits occur. The primary argument that has been pitched against MLS is that these conditions of low within-group variance and high between-group variance are rarely met in most naturally occurring species. Proponents of cMLS have presented strong evidence that this argument does not apply in the case of culturally transmitted traits, because human psychology and cultural norms tend to maintain between-group differences (Boehm 1997; Boyd & Richerson 2005; Chudek & Henrich 2011; Henrich 2004a; Laland et al. 2000).

In discussing the adoption of the cMLS perspective, Laland et al. (2000) have written: "Group selection of cultural rather than genetic variation requires a 'frame shift' of replicator, because it is not genes that are selected for, but rather groups of individuals expressing a particular cultural idea" (p. 143). Nevertheless, the traits in question in the cMLS perspective – whether "cultural ideas" or the more behavioral "cultural variants" (Richerson & Boyd 2005) – exist at the level of individuals. Although fitness may be evaluated at the group level by averaging across group members, each trait in question is still the property of individuals in that group. I argue that the frame shift proposed by Laland et al. (2000) is not incorrect, but it is incomplete. The cMLS view does not at present account for the fact that collaborative behaviors, requiring differentiated and structurally organized roles, have played an essential role in the success of human groups. Group-level traits exist fundamentally at the level of groups and can therefore only be defined in those terms. A group may be partially successful because its members express a particular cultural idea. But a large part of group success comes not from an aggregate of identical individuals each expressing a unitary idea, but from the organization of a

well-defined collection of differentiated individuals all participating in a group-level behavior, as in the case of the Roman Legion.

A related view has been advocated by MLS theorists seeking to distinguish between effects of group structure on the fitness of either (1) the constituent individuals or (2) the groups themselves, with the former view designated MLS1 and the latter MLS2 (Damuth & Heisler 1988; Michod 2005; Okasha 2005, 2006). On the surface, MLS2 may appear to be the appropriate framework for discussing the evolution of human group-level traits. Indeed, some presentations explicitly discuss emergent traits as properties of the collective group, rather than belonging to the individual group constituents. However, these "emergent" traits are, in general, aggregate properties of the collective as a whole, rather than produced by interactions among its members. Two examples given by Okasha (2006) are (a) the geographical range of a species of mollusk and (b) the degree of morphological differentiation between castes in a colony of social insects. These traits are to some degree emergent in the sense discussed by Wimsatt (1997; 2006), yet both exhibit aggregate quality 1, in that they are invariant to a rearrangement of parts. Example (a) does not depend on either differentiation or organization – but only on the sum of the ranges of the individual species members. Example (b) describes differentiation and organization. However, the trait does not *emerge* from the collection of individuals possessing those properties, but is merely a statistical description of their organization. As such, the MLS1/MLS2 framework is not yet well developed enough to account for the evolution of group-level traits. Moreover, as discussed earlier, human trait-groups are not fixed collections but are defined by the traits themselves. Individuals may become involved in many groups, with varied memberships and purposes, throughout their lives. Thus, although patterns of organization and differentiation may propagate through culture and social learning – discussed in more detail in

subsequent sections – a trait-group is not itself consistent enough over time to constitute a unit of selection as defined by MLS2.

Several authors have previously discussed group-level traits produced by organization and differentiation in the context of human cultural evolution (e.g., Boehm 1997; Caporael 2001; Henrich 2004a, 2010; Richerson & Henrich 2012; Wilson & Sober 1994). However, these authors have typically failed to acknowledge a special significance of such traits and have instead discussed them as equivalent to aggregates of individuals all exhibiting individual-level traits (i.e., *not* defined by organization and differentiation). For example, Wilson and Sober (1994), in their famous paper "Reintroducing Group Selection to the Human Behavioral Sciences," write: "It is also crucial for our hypothesis that group-level functional organization is, in some sense, superior to what can be accomplished by individuals when they are free to pursue their own self-interest" (p. 604). Yet the idea of "group-level functional organization" is not explored further in their paper.

Some considerations of cultural group selection have gone beyond ignoring within-group differentiation and have actively argued for the importance of within-group homogeneity. Boehm (1997), for example, has made this suggestion in his discussions of "egalitarian behavioral syndrome" in small-scale societies, which involves moralistic norms to control antisocial behavior and thereby dampens within-group phenotypic variation and amplifies variation between groups. The argument focuses on the fact that egalitarian norms allow maximal sharing of resources, which in turn purportedly maximizes group success. However, this argument holds only as long as the baseline fitness, beyond the sharing or withholding of individual resources, is constant between groups. Any fitness gains (or losses) based on group organization will be missed by cMLS models that do not consider the influence of within-group differentiation and

organization. In contrast, such within-group differentiation allows for the emergence of group-level traits and can thereby permit structured groups to have an evolutionary advantage over similar groups with more homogeneity and less emergent structure. Although selection on both biological and cultural traits may favor homogeneity in some cases, such as in the emergence of early hunter-gatherer societies, the historical record emphatically supports the conclusion that structured differentiation is often beneficial to group success.

4. Beyond cooperation

The majority of the theoretical and empirical literature on social and cultural evolution, in humans as well as other species, has focused on cooperation. This stems in part from the seemingly mysterious questions of how cooperation can first evolve and how it can be maintained. After all, if I help you at a cost to myself and you do not reciprocate, then I suffer a cost and you reap all the benefit. Half a century of research on cooperation has largely solved this puzzle. Cooperation can evolve if individuals with heritable cooperative tendencies can positively assort (Fletcher & Doebeli 2009; Smaldino & Schank 2012a; Wilson & Dugatkin 1997), meaning that they tend to interact more with one another than at random. Positive assortment can be facilitated by a variety of mechanisms, including kin recognition, cognitive bookkeeping (McElreath & Boyd 2007), spatial assortment with limited dispersal (Koella 2000; Smaldino & Schank 2012a), or goal-directed movement away from free riders (Aktipis 2004; Helbing & Yu 2009; Smaldino & Lubell 2011). Free riders will of course be a perennial problem, in part because the relative benefit of free riding increases with the frequency of cooperators. However, once established, cooperation can be enforced by social institutions such as direct reciprocity (Trivers 1971), indirect reciprocity (Nowak & Sigmund 2005), reputational exclusion (Smaldino & Lubell, in press), and punishment (Boyd & Richerson 1992; Henrich &

Boyd 2001).

So, although there are still open questions related to the evolution and maintenance of cooperation, its presence is no longer a mystery. Its ubiquity in human society, far beyond that found in other species, presents perhaps more of a puzzle. Humans live in large groups of unrelated individuals and are inherently group-minded. The question often posed is: How is it that we cooperate so much? Proponents of cultural group selection have argued forcefully for a two-step process (Chudek & Henrich 2011; Richerson & Boyd 2005). First, cultural learning biases (e.g., conformity, learning from prestigious individuals) and a suite of psychological mechanisms evolved for dealing with social norms combine to maintain within-group similarity and between-group variation. Second, competition between groups selects for groups with cooperative social norms. Although the logic of this process is sound, it also downplays the important role of within-group variation in making groups of individuals working together so successful. For example, norms of organization and differentiation may not be fully carried in the minds of individuals, but may be transmitted through inheritance of social structure (Laland & O'Brien 2012), as well as through the maintenance of variation within the population to produce individuals who take on differentiated roles.

4.1. Cooperation vs. collaborative interdependence

In the Russian arctic, Inuit hunters forage for seabird eggs during the summer months when seals and walrus are scarce (Fothergill & Berlowitz 2011). These birds nest on sheer cliffs, making accessing their eggs a challenge. The hunters' solution is to fasten a strong rope to the waist of one individual and to have the other members of the team lower him down the cliff to collect eggs into a leather bag. Adjustments in the rope tension are made through verbal communication, and the climber is pulled up when his bag is full. Through this collaborative exercise, enough

eggs can be collected to feed all the hunters and their families. In many respects, this activity is obviously a cooperative behavior. Each individual is contributing time and energy to a common good. Yet, the group-level behavior is defined not simply in terms of individuals donating or withholding contributions, but in terms of each individual doing his own part in a coordinated and organized manner. These hunters are doing more than cooperating: they are collaborating.

Much of the work on the evolution of cooperation is based on social dilemma games such as the prisoner's dilemma, public goods, snowdrift, and stag hunt games, and research tends to focus on how to evolve and sustain general practices of cooperation. An implicit assumption of the payoff structures of these cooperative games is that cooperative or altruistic acts are completely general; that is, interacting with one cooperator is just as good as the next. Some work has considered cooperation only between members of the same group (Antal et al. 2009; Axelrod et al. 2004; Hammond & Axelrod 2006; Jansen & Van Baalen 2006), but acts of cooperation within groups are still treated as equivalent. This structure misses a couple of important points about how cooperation works in human societies. The first is that cooperation is often domain specific. For example, some Indian villagers have been known to cooperate across castes in some domains (e.g., farming) but not others (e.g., marriage) (Waring 2012).

The second and much richer point is that with whom one cooperates matters. It matters not only to the individuals involved, but also to other members of the group. Generically, assume individuals A, B, and C are all members of a larger group, and further assume that they all tend to cooperate with members of their group. Whether A chooses to interact with B or with C matters, not only for A's individual payoff, but also to the quality of the public good available to A's group. In other words, some structural relationships are more productive, in absolute terms, than others. As an example, consider a hypothetical small-scale society of arctic hunters. A seal

hunter and a kayak builder have a high incentive to cooperate with one another. They have each developed skills that require those provided by the counterpart. If the kayak builder gives the seal hunter a boat, he can be rewarded in turn with sustaining meat. The kayak builder has a very different relationship with a rival kayak builder, who may cooperate by sharing knowledge or building materials, but also competes for customers (and therefore the returns from hunting voyages). Moreover, the seal hunter should choose carefully with which kayak builder he cooperates. If he chooses one with less skill, he may have to expend more time and resources to guide his craft on the water and to repair it if it is more prone to damage. This will lead to a less fruitful hunt and to less food for the group overall. For a related discussion, see Calcott (2008).

Some work on game-theoretic models of cooperation may tacitly assume that differentiation and specialization are sources of the non-zero sum nature of scenarios such as the prisoner's dilemma. The omission of individual-level diversity and differing payoffs for different constellations of collaborators is often a useful simplifying assumption. Nevertheless, an inclusion of that diversity will help to shed a brighter and broader light on the forces underlying human evolutionary success, not only for evolutionary researchers, but also for students learning to think about human cooperation through the abstractions of game-theoretic models. The real story of how large-scale cooperation became established during the evolution of behaviorally modern humans is likely to have involved a trajectory of organization and differentiation that cannot be captured by more traditional cooperation models. As humans evolved to live in groups, group behaviors such as cooperative breeding and collective foraging allowed them to adapt to environments too harsh to sustain noncooperative individualists (Bergmüller et al. 2007; Hill & Hurtado 2009). Eventually, such adaptations may have created the necessity for interdependence, in which survival without some minimal amount of cooperation or aid from other group

members was impossible (Smaldino et al. 2013; Smaldino et al., submitted). Interdependence sustains cooperation and provides a stable environment of mutual aid in which differentiation, division of labor, and complex group organization can emerge.

The simplest form of interdependent collaboration stems from a diversity of abilities when a group is engaged in a common endeavor. Diversity creates a broader base of ideas for solving problems and innovation. Organization and management scientists have shown that for a variety of problems, problem-solving teams whose members exhibit diversity in training background and styles of thinking are often more effective than teams consisting of experts in any one area (S. E. Page 2007; Post et al. 2009). Henrich (2004b) has also shown that greater diversity in observer inferences during social learning can promote adaptive cultural evolution for individual-level traits.

Over time, even subtle differences in abilities and circumstances can give rise to differentiated individuals who are dedicated in their roles and deeply specialized. Formal division of labor is required for many group-level behaviors. Division of labor allows specialized individuals to achieve depths of skill impossible for the generalist. A group with division of labor can easily outperform a group of generalists, but only if those specialists reinforce one another by providing what others lack.

In this light, cooperation becomes more nuanced and gives way to collaboration, in which specialized individuals form an interdependent network of skills, personalities, and experiences that all contribute to group success. This also suggests a reconsideration of the value some researchers have placed on egalitarian norms (Boehm 1997; Wilson & Sober 1994). For example, Wilson and Sober (1994) discuss the Hutterite society, a communal branch of Anabaptists that originated in Central Europe in the sixteenth century. Hutterites place high value

on egalitarianism, which minimizes within-group variation and should, in the cMLS framework, promote group success. But this view can also overlook the importance of differentiation and organization within groups, which are essential for generating group-level traits. Wilson and Sober remark that in present-day (i.e., 1994) Canada, "Hutterites thrive in marginal farming habitat … and would almost certainly displace the non-Hutterite population in the absence of laws that restrict their expansion" (p. 605). Wilson and Sober (1994) are arguing not only that egalitarians norms have driven the success of the Hutterites, but also that it is lucky for Canada that its government has regulatory laws in place to stem the otherwise unstoppable tide of Hutterite expansion. In my view, a key element of this story is that the more "mainstream" society of Canada and its government possess organizations such as regulatory agencies and law enforcement that permit a seemingly effortless impediment to Hutterite expansion. Canadian culture in this sense outcompetes Hutterite culture not through increased norms of cooperation, but via properties that emerge from complex social organization. It is clear from models and from studies of small-scale societies that, in a population of near-equals, increased cooperation and egalitarianism can promote group success. When dealing with complex societies, however, a focus on cooperation is limited because it misses the influences of collaborative interdependence and group-level traits. This point is supported by a recent game-theoretic model demonstrating that economic stratification and division of labor within a structured society could generate higher total group payoffs than egalitarian norms (Henrich & Boyd 2008). Importantly, such a payoff differential creates the conditions for selection between groups. Moreover, Henrich and Boyd's (2008) model provides a rare example of an explicit evolutionary model of cooperation among differentiated individuals. The authors assumed that all interactions were cooperative but posited different payoffs for different dyadic pairings. Further work on the evolutionary

significance of interdependent collaboration will be illuminating.

The aim of this discussion is not to downplay the importance of cooperation in human evolution. Cooperation is essential in many contexts of human life, and the value of promoting cooperation and deterring free riding should not be understated. Nevertheless, cooperation only gets us part of the way to explaining the emergence and sustainability of complex group-level behaviors. Once cooperation between individuals evolves, the stage is set – via persistent association, interdependence, and cultural transmission – for the evolution of nuanced collaboration between individuals with differentiated roles in a meaningful social organization.

5. Explaining the emergence of group-level traits

Group-level traits allow groups to do things that aggregates of individuals cannot do otherwise. Humans build skyscrapers, sail ships, and create complex tools, infrastructure, and modes of transportation. We pass down traditions of learning that enable cumulative improvements and innovations, including knowledge that no single generation of social learners could acquire on its own. How do complex group-level traits emerge from properties and behaviors of individuals?

The eusocial insects, which includes many species of ants, termites, and bees, also exhibit group-level traits with differentiation and organization. The construction and defense of ant bivouacs or giant termite mounds are neither the product of a single individual nor that of an aggregate of identical workers. Rather, it takes the interdependent collaboration of workers and soldiers, drones and queens. Eusocial insect colonies, however, are collections of individuals with a high degree of genetic relatedness, and the emergence of group-level traits in these species is encoded at the level of the genotypes of the foundress queens, their mates, and their offspring.[1] The colony is in some sense an extended phenotype of the queen (Reeve & Hölldobler 2007), with between-group differences explained by genetic (and also environmental) differences, and

within-group differences explained by variation in environmental stimuli, triggering differential gene activation during development. In contrast, group-level traits in humans are transmitted culturally rather than genetically, requiring different explanations for their emergence and evolution. In this section, I focus on proximate mechanisms that contribute to the emergence of group-level traits.

Uniquely, humans live in large, complex societies full of cooperative and collaborative relationships between non-kin, and so the extended phenotype explanation does not apply to selection on human group organization. Humans seem built to learn from one another, and most differences between groups of humans appear to be largely the result of learning rather than genotype (Richerson & Boyd 2005; Richerson et al., in prep). This statement is well supported by the empirical literature on human development (Chudek et al. 2013; Harris 2012; Richerson et al., in prep) and cultural psychology (Nisbett et al. 2001; Nisbett & Miyamoto 2005). Even the mother-infant attachment relationship, which is for most humans their first participation in a group-level trait and is in many ways a human universal (Grossman & Grossman 2006), is influenced by the culture and past experiences of the mother (van Ijzendoorn et al. 2006). Is it possible that group-level traits are fully explained by socially learned individual-level traits? In order to explain group-level traits, the emergence of differences among individuals within a single group, and the subsequent organization of those differentiated individuals and their coordinated behavior must be accounted for. Bearing in mind the complications involved in the proximate/ultimate distinction[2] (Laland et al. 2011), three possible proximate explanations for the emergence of group-level traits present themselves. Each is only partly explanatory on its own – a fuller picture requires the incorporation of all three.

5.1. The role of leaders

First, some individuals may possess a plan or leadership quality that allows them to direct others into some organization and guide them through a task. Indeed, a person can – and often does – carry around large portions of the roles, rules, interactions, and institutions for group-level traits in her mind. Not only that, but the individual can use that information to predict how a group will behave under such a structural organization. Indeed, much of modern social science has been dedicated to the conceptualization and description of the ways in which organizational changes will affect group outcomes. The crux, however, is that individuals cannot *express* those group-level traits. To do so, they need a collective of cooperative, differentiated individuals. They have to start a company, form a band, inspire a religion, lead a nation. This sort of behavior is at the heart of modern human history.

Moreover, it is often impossible to precisely guide other individuals to perform exactly as one wishes. An old adage in the film industry is that "good directing is 90 percent casting." In other words, getting the right group of people in the right roles is essential for achieving good results. This is not to suggest that individual leaders, such as directors, architects, and CEOs, are not important to the operation of group behaviors. Rather, their roles are limited by other forces, including not only the characteristics of the other individuals involved, but also the constraints related to environment, infrastructure, and culture. Furthermore, leadership does not explain the existence of suitable differentiated individuals to perform a given task.

Maynard Smith and Szathmary (1995) contrast the function and complexity of a termite mound with that of a human building, noting that although the two resemble one another in many ways, the termite mound "differs in that not one of its builders had a picture of the completed structure before building started" (p. 257). Although many of the people involved in

manufacturing human constructions have a mental picture of the finished object, it also true that, in many cases, no single person has either the knowledge or the ability to build that object. This was noted by the economist Leonard Read (1958) in his whimsical essay "I, Pencil" in which he suggests that no single person can make something so seemingly simple as a pencil. Indeed, much of the technology in the developed world is so complex and built on cumulative technologies, designs, and materials that thousands if not millions of individuals may be involved in their construction, none of whom know how to make the completed product (and few of whom may ever use or even see the completed product!) (Ridley 2010).[3] Therefore, although important, planning and leadership cannot fully explain group-level traits.

5.2. The emergence of division of labor

Second, although individuals may all be exposed to the same socially transmitted information via common cultural environments, environmental and biological differences may create the opportunities for differentiation. Differentiation and division of labor may emerge when small differences are exacerbated through the exploitation of opportunities. R. E. Page and colleagues (Fewell & Page 1999; Page & Mitchell 1991) have developed a model of division of labor in insect societies in which differentiation emerges when intrinsic variation exists in the ability to perform a behavior and performing that behavior reduces the need for others to complete the specific task. It seems reasonable to propose that some differentiation in human societies may also be explained in this way. For example, most competitive Canadian hockey players are born in the first few months of the year (January, February, March). This is not because of astrological providence, but rather because January 1 is the age cutoff for most youth hockey leagues. In these leagues, players born earlier will tend to be bigger and stronger than their co-players and will tend to perform best and, subsequently, will have more opportunities and more coaching,

widening the performance gap (Gladwell 2008). Since not everyone can play in the pro leagues, some players will get dropped, and on average, rosters will include more players born early in the year. The widening of intrinsic differences through education and experience therefore creates opportunities for differentiation. Here, selection can operate at the individual level, with a frequency dependency for various phenotypes depending on the priority of the organizational roles to which those phenotypes are best suited. However, two questions illustrate that this is not a complete explanation of group-level traits. First, how do opportunities for improvement in a given role arise? That is, how are individuals selected for specific roles, and how do they get their role-specific training? Second, and more importantly, where do the available roles come from in the first place? A hockey player can only play hockey if opportunities to do so are available and can only turn professional if pro hockey leagues exist. Similarly, a soldier must be trained in an active military establishment or by cultural traditions of warriorhood, and a novice canoe builder must generally be taught by an elder canoe builder.

5.3. Repeated assembly

A third explanation for group-level traits incorporates the facts that humans have cumulative culture, a long developmental trajectory, and lots of generational overlap. Group-level traits may be examples of what Caporael (2003) has termed *repeated assemblies.* These are "recurrent entity-environment relations composed of hierarchically organized heterogeneous components having different temporal frequencies and scales of replication" (Caporael 2003, p. 77). The repeated assembly view as applied to individual development stands in counterpoint to the view that contributions from genotype ("nature") and environment ("nurture") may be viewed additively or, at best, as interacting in fairly simple ways; this latter view characterizes some work in evolutionary psychology (e.g., Tooby & Cosmides 1992) and behavioral genetics

(Bouchard & Loehlin 2001; Kendler & Greenspan 2006). Instead, development is characterized by a process by which the individual is assembled in overlapping cycles – aspects of the current cycle seed the beginning of the next – with cycles occurring at varying timescales and involving varied interactions between the individual, the external environment, and other social interactants. Stages of development may be scaffolded by more experienced individuals, as well as environmental and cultural structures that promote learning and transitions to subsequent stages (Wimsatt & Griesemer 2007). The development of organized groups, exhibiting emergent group-level traits, may occur in a similar manner. A major difference is that the components of the group may change over time, while the group's structure may change little. The inverse may also occur: group structure may change even though the constituents do not, or the constituents may change only in the sense that the same individuals change roles to fit a new structural organization. The evolution of such organizational structure is therefore qualitatively different from selection on individual-level traits.

Consider also the importance of pedagogy and the development of social roles. In any given social context, individuals may have roles related to the structure of the organization and the needs of the related endeavor. These roles may be entrenched in tradition and infrastructure, but they may also be in near-constant flux. Adult humans do not spring into existence fully formed with a set of relevant skills. Throughout their development, individuals are drawn to different roles through opportunity, experience, and epigenetically developed predispositions (Gottesman & Hanson 2006; Nijhout 2003; Simonton 1999). As novices in an organization, they learn by instruction, imitation, and exposure from more experienced individuals. Once they themselves become experienced, they may take on the role of mentor to more junior members of the organization, and there is no reason this scaffolding cannot be multitiered.

Human cognition is highly adapted for social coordination, to a much greater extent than our nearest primate relatives (Herrmann et al. 2007). Although chimpanzees may engage in collective behaviors, such as those for hunting or defense, Tomasello and colleagues (2005) have argued that "in these interactions each individual does basically the same thing, they just do it in concert" (p. 685). In contrast, humans collaborate in organized groups of differentiated individuals, and much of our evolved psychology is related to the fact that we live in social groups – perception, cognition, and behavior relating to social relationships are paramount (Brewer 2004; Caporael & Brewer 1995).

Humans have species-specific cognitive and perceptual mechanisms that allow for scaffolded social learning, which likely facilitated the emergence of cumulative culture (Csibra & Gergely 2011; Moll & Tomasello 2007; Tomasello et al. 2005). These psychological mechanisms likely coevolved through mutual reinforcement with social structures that promoted coordinated communication and organization (Gong & Shuai 2012), allowing generations of early hominins to develop organizational structures of increasing complexity over many generations. In general, modern humans have deep-rooted dispositions toward cooperation and collaboration, far beyond those of other species (Bowles & Gintis 2011; Nowak 2011; Richerson & Boyd 2005; Tomasello 2009). Once these collaborative instincts are present, different distributed collective adaptations – group-level traits – can be transmitted among groups, because people remain largely unspecialized in morphology but can become extremely behaviorally specialized during development.

6. The maintenance and evolution of group-level traits

People do not simply assess and imitate individual behaviors. They adopt entire suites of behaviors, perceptual norms, and decision heuristics (e.g., "What would Jesus do?"). Norm-

enforcing institutions allow suites of cultural traits to be transmitted wholesale, which in turn allows for something analogous to natural selection to operate on the group-level traits that emerge from cohesive collections of individual-level traits. Mechanisms that stabilize group-level cultural identities have been well documented. For example, initially arbitrary ethnic markers can evolve and stabilize because they help facilitate within-group interactions, which tend to be more important than extra-group interactions (McElreath et al. 2003). Durham (1991) discusses a number of ecological, psychological, linguistic, and cultural barriers to the blending of cultures, which he terms *transmission isolating mechanisms* (TRIMs). These mechanisms ensure that cultural identities remain relatively stable, even when individuals from different cultures interact. TRIMs are the major reason that cultural evolution at the level of groups, in the cMLS sense, can occur. TRIMs also help to stabilize the differentiated roles needed for the successful functioning of an organized group-level trait. As a simple example, positions within a formal organization may only be filled when there is a vacancy, and there are incentives to perform one's stated role and not impinge on another's responsibilities.

Mechanisms also exist that allow within-group differences and patterns of organization to be maintained and transmitted. For example, narrative stories and other media are important factors in the preservation of cultures and customs. An important but rarely made point about the role of narrative in human evolution is that a cultural tradition of story and mythology gives the members of a culture common referents – a perceptual lens through which to assess and communicate a particular situation. This claim is supported by evidence that culture and social learning can have important influences on basic cognitive and perceptual functioning.

L. F. Barrett and her colleagues have proposed that the common emotion categories (e.g., fear, anger, happiness) are not true natural kinds, but rather emerge through attractor states that

arise as neurobiology is shaped by language and culture (L. F. Barrett 2006; L. F. Barrett et al. 2007; Lindquist et al. 2012). In other words, different neurophysiological states may lead to similar arousal levels and may be cognitively and phenomenologically mapped as a particular emotion. This process of fast categorization may aid in the adaptive rapid assessment of a situation and may interact with fast and frugal decision-making heuristics (Cunningham et al. 2007; Gigerenzer et al. 1999; Smaldino & Schank 2012b). Analogously, there are myriad ways in which humans can perceive any given set of circumstances. Perception is constrained in part by our biology, but culture also constrains even our basic perceptions of a situation (Nisbett & Miyamoto 2005; Smaldino & Richerson 2012). For example, Masuda and Nisbett (2001) showed American and Japanese university students animated underwater scenes with a focal fish. In a recall task, Americans were much better identifying fish they had seen independent of background information, but Japanese students were much better at remembering details of the background scenes. Cultural differences in patterns of perception and memory fit larger cultural differences in epistemology and styles of thinking that exist between East and West (Nisbett et al. 2001). Nisbett and Miyamoto (2005) have even proposed that cultures tend to shape their own environmental landscapes to reinforce cultural perceptive norms.

If culture can influence how members of that culture perceive situations, then culturally transmitted norm-enforcing institutions should indicate norms of organization and roles within those organizations. Narratives, mythologies, and other media take on the important role not only of maintaining differences between cultural groups, but also of maintaining differences between individuals within groups and organizational structures for those individuals. Institutions that transmit these patterns of organization are in some (very loose) sense the vehicles through which group-level traits are transmitted.

6.1. Religion as a norm-enforcing institution

Dennett (2006a) has proposed that "the key to our domination of the planet is culture, and the key to culture is religion." Although I believe that religion is only one among a number of important norm-enforcing institutions, it has also historically been a particularly effective mechanism for transmitting whole suites of cultural norms. Religion may be viewed as one of the primary methods by which a culture maintains its norms of social organization and by which it propagates those norms (Wilson 2002; Atran & Henrich 2010). In a now-classic study, Cavalli-Sforza and colleagues (1982) found that religious traits are among those most strongly influenced by vertical transmission, especially between mothers and offspring. Religious identity is therefore both highly susceptible to cultural transmission and unlikely to change through adult peer influence. This may partly be because religions are highly entrenched in cultures as a force for the differentiation and organization of individuals and are thus more difficult to change compared with institutions that only affect individual-level traits. However, large-scale religious conversion is not unknown. In this way, a suite of individual-level traits and organizational norms can be transmitted wholesale from one cultural group to another.

There is a particularly enlightening historical example of a suite of cultural norms being *mis*-transmitted from one group to another, because the two cultures lacked sufficient common ground (Clark & Brennan 1991) to effectively understand the context of the other's organizational roles. These are the famous cargo cults of the Pacific Islands, and they provide an example of something analogous to mutation in the transmission of group-level traits (Dennett 2006b). A number of times in the last few hundred years, Europeans and Americans landed and set up shop on certain Pacific Islands, which were home to small-scale societies with traditional practices of ancestor worship. Some of the (often arbitrary) organizational traits of the Westerns

were perceived by the islanders as practices through which their gods must have given them "cargo," a blanket term denoting the Westerners' wondrous material wealth. During World War II, Americans set up a base on the island of Efate and recruited workers from among the islanders of nearby Tana. Soon the people of Tana, having heard tales of the colossal wealth and technology of the Americans, began marching in parades, marking "USA" on their chests, and carving bamboo figurines of American warplanes, helmets, and rifles for use as religious icons. During festivals, elders would perform a dance based on American military drills. This was ostensibly in hopes that whatever gods bestowed cargo on the Americans would bless them similarly. What is especially fascinating in these examples is that not only were individual behaviors transmitted, but so were complex group-level traits and patterns of role differentiation. Islanders built plane runways, with some individuals stationed as flaggers and others up in towers wearing headphones made from coconuts (White 1965). The cargo cultists appear to have gotten the idea that, in order to receive cargo, they needed to do more than adopt particular behaviors – they needed to adopt particular social structures. This is significant, because social transmission of behavior is typically assumed to occur at the level of individuals. Here instead we see the transmission of social organization.

6.2. The adaptiveness of group-level traits

Modern Christian religions provide an example of how group-level traits might propagate more reliably. Religious organizations often include the office of missionary, in which church members are rewarded for bringing new individuals or, even better, new communities into the fold. The Church of Latter-Day Saints (LDS, Mormon) has gone so far as to make missionary work a developmental stage in the lives of all its members, which may partially account for why LDS is one of the fastest growing religions in many parts of the world (Grammich et al. 2012).

As another example, consider Catholicism, which has been so important to the success of certain cultural groups (and remains so in some parts of the world). There, functional differentiation of roles has given rise to the priesthood, a set of individuals whose genetic fitness is zero but who exert a major influence on the cultural transmission of the norms and group-level traits associated with the Church. Direct proselytizing is only one way, however, by which group-level traits may spread.

Norms that facilitate more effective group organization will spread because the groups that exhibit the associated group-level traits will outperform groups with less effective organization. The Roman Legion will defeat the Barbarian Horde nine times out of ten.[4] This principle of organization triumphing over sheer numbers is itself a common trope in Western cultural narratives. Consider, for example, the number of films in which a ragtag group of scrappers beat some sort of corporate behemoth by cunning and coordination. In this way, a focus on group-level traits may become more likely to guide organizational decisions.

Some group-level traits may promote not only themselves, but also the persistence of other cultural traits (including other group-level traits), in a manner similar to genetic linkage. For example, democratic norms, by which the citizenry vote on policy choices, can maintain many normative aspects of a culture because ideas that represent large deviations from the status quo are unlikely to receive a majority of votes (Nagel 2010). On a smaller scale, consider a musical group. A rock band is not a collection of individuals all with a "musician trait." Rather, the individuals play different instruments and often have quite different skills and qualities. The collectively formed musical group exhibits group-level traits that not only propagate themselves (in the spread of the music and the formation of future bands), but also ideas and norms associated with both the music and personalities of the individual musicians, band identity, and

related subcultures. Returning to the subject of religion, Atran and Norenzayan (2004) have persuasively argued that religious rituals, which tend to involve specialized roles (Barrett 2000), often serve an important function in maintaining group cohesiveness and commitment to the group's welfare among its constituents.

6.3. Technology and the adaptive response of group-level traits

Groups of humans can differentiate and organize based on learned traditions and the interplay between biological predispositions and cultural opportunities. However, many group-level traits also rely on characteristics of the environment, including the social environment, which can irrevocably change from one generation to the next. Perhaps the simplest characteristic of the social environment is population size. Isolated from mainland Australia after the seas began to rise after the last glacial period, humans on Tasmania were stranded on an island that could not sustain more than a few thousand people. Over several thousands of years, the Tasmanians lost previously held technologies (e.g., bone tools) and never evolved others (e.g., cold-weather clothing, fishing hooks) that readily developed in Aboriginal communities on the Australian mainland (Davidson & Roberts 2009; Diamond 1978; 1999; Henrich 2004b). Isolated from the mainland, they had no influx of new technologies and too small a population to successfully sustain their existing complex technologies. Recent theoretical work has suggested that if complex technologies are more difficult to learn and individuals vary in their ability to imitate the best among them, then complex skills can fade away in small populations (Henrich 2004b; Powell et al. 2009; but see also Read 2006; Vaesen 2012). This pattern of technology loss as a result of a shrink in population size has also been observed in several other populations (Boyd et al. 2011), and a recent analysis of indigenous marine foraging societies of Oceania found that both population size and contact with other populations predicted the technological complexity

of their toolkits (Kline & Boyd 2010). The evolution of complex group-level traits may therefore require some threshold population size in order to generate sufficient numbers of organized and specialized individuals. As such, technological complexity can be properly considered a group-level trait.

How are technologies maintained? Clearly, cumulative social learning and innovation across generations are necessary to build many things that a single human being could not invent from scratch. Beyond this, however, social networks, division of labor, and cultural traditions also contribute to the maintenance of innovation. Recall the earlier discussion of the complexity of the pencil. Certain types of organizational structures might be necessary to maintain even simple technologies. A sufficiently large population is, in turn, necessary to maintain the levels of complexity in differentiated social networks required to sustain complex technologies. Because complex technology often requires significant division of labor, the costs of specialization may be outweighed by the gains only when the specialist has enough customers and collaborators to be meaningfully useful. Thus, as the population of Tasmanians fell (and lost contact with outsiders), the group-level traits necessary to sustain innovations were no longer possible.[5] This makes further sense if we consider an inverse situation: the vastly complex technologies of the modern developed world. How many hundreds of millions of interconnected individuals are necessary to sustain the Internet? Smartphones? Airline travel? Innovations are abundant and sustainable precisely because our population is so large and intertwined.

7. Moving between the levels of selection

Human societies are high in what Wimsatt (1974) has called *interactional complexity*. Roughly, this means that an investigator wishing to make useful predictions must simultaneously consider the system from multiple descriptive perspectives, because elements of those different

perspectives interact in a causal manner. We can describe societies at the level of individuals, in terms of nuclear families, kin groups, subcultures, and social classes. We can also include infrastructure and transportation, livestock and farming, religious rituals and linguistic traditions, and all this is on top of the descriptive complexity of an individual human. A complex society cannot be adequately described in terms of any single descriptive decomposition. In order to better characterize the behavior and evolution of human societies, we must move beyond a simplistic multilevel viewpoint that portrays groups as aggregates of relatively undifferentiated individuals and thus implies that it is coherent to speak of the "group level" and "individual level" separately. Groups are complex organizations of differentiated individuals, and individual behavior is constrained by group organization.

Some perspectives on social and cultural evolution have recently emerged that accept the idea that organization matters in evolutionary models. Certainly, plenty of work on spatial organization and mobility within and between groups has shown that these factors influence evolutionary dynamics (Durrett & Levin 1994; Lion & van Baalen 2008; Perc & Szolnoki 2010; Smaldino & Schank 2012a). Work on niche construction (Laland & O'Brien, 2012; Laland & Sterelny, 2006; Odling-Smee et al. 2003) has formalized and extended Lewontin's (1982) observation that individuals actively alter their environments, creating new selection pressures that can be inherited by subsequent generations. Even more recently, discussion has turned to an emphasis on developmental scaffolds as a force in cultural evolution (Caporael et al., in press; Wimsatt & Griesemer 2007), though this perspective has not been extensively modeled. Still, a between-levels perspective in which groups and individuals are separate but intrinsically connected and in which the organization of differentiated individuals creates new group-level traits has yet to be addressed.

7.1. Group-level traits, MLS, and inclusive fitness

Traditional formulations of MLS (MLS1) treat group effects in terms of positive assortment – in-group members assort, so the fitness of an individual is influenced by the individual fitness differential of its own traits plus the fitness differential provided by the social traits of its group members. Thus, an altruistic trait that extracts a cost from an individual but benefits group members can evolve if the degree of in-group assortment is high enough. As many have pointed out, this formulation is mathematically equivalent to an inclusive fitness approach that accounts for the degree of assortment without explicitly accounting for group structure (Bijma & Aanen 2010; Bourke 2011; Marshall 2011; Wild et al. 2009; Wilson & Dugatkin 1997). Nevertheless, many proponents of cMLS theory have argued that studies of human cultural evolution and gene-culture coevolution are best served by a perspective that accounts for group structure (Chudek & Henrich 2011; Henrich 2004a; Laland et al. 2000; Richerson & Boyd 1998; 2005). The arguments presented in this target article support this position and take it a step further. When it comes to human cultural evolution, the equivalency between MLS and inclusive fitness theory dissolves once a between-levels perspective incorporating group-level traits is adopted.

When group-level traits can emerge and be maintained through processes that do not require genetic relatedness, an individual's social environment cannot be reduced to the frequencies of various social phenotypes. Rather, the social environment includes the structured groups (exhibiting group-level traits) in which the individual participates, as well as those groups that influence the fitness and behavior of both the individual and her groups. Individuals partner with other differentiated individuals in an organized fashion, constrained by institutional and developmental processes. This organizational complexity means that accounting for the degree of assortment between individual trait types is insufficient to calculate fitness. It follows that a

multilevel selection theory of cultural evolution that incorporates emergent group-level traits is not equivalent to an inclusive fitness approach that focuses only on individuals and aggregate conceptualizations of fitness in groups.

8. Future directions

The idea that the structured organization of differentiated individuals influences the behavior of human groups is not new. Cultural anthropologists, for example, have long recognized the importance of characterizing multiple levels of organization in their descriptions of cultures (e.g., Hinde 1976). The fields of management science and organizational psychology are almost entirely devoted to studying aspects of the organization and dynamics of groups. In discussions of cultural evolution, however, group organization is often ignored. By ignoring the role of group-level traits in cultural evolution, as well as the evolution of those traits, researchers have overlooked a major force in the ecology and evolution of human societies. This is particularly true when attempting to extend cultural evolution theory beyond small-scale societies and into the more developed civilizations of the past 5,000 years. If complex organization and differentiation of roles were key factors in the cultural and genetic success of those peoples, then those factors should be examined head on.

A pressing problem concerns the understanding of how group-level traits are transmitted and how the relevant patterns of organization adapt and change. Other important problems involve the identification of cooperative and collaborative organizations that have culturally evolved, understanding how those organizations are related to each other, and incorporating in this framework how individuals can participate in multiple group organizations at the same time. Studying group-level traits in ecological and evolutionary contexts may require new methodologies or, minimally, the alteration of existing methods. A detailed outline of such

methods is beyond the scope of this target article, but several possibilities readily present themselves. A general challenge for mathematical biology is the search for better ways to model multilevel systems (Cohen 2004). A focus on the emergence and evolution of group-level traits provides a suite of interesting problems for mathematical scientists. For example, models are needed that capture the difference between the social spreading of a particular individual-level trait and the emergence of group-level behaviors that rely on differentiation and organization. There is also a need for methods for identifying the presence of group-level traits and their evolutionary and developmental trajectories, as well as their effects on the evolution of individual genes and cultural variants (and vice versa). Theorists should work to develop models for how groups form, evolve, and coevolve with individual-level traits. Another important avenue of research concerns the influence of cultural niche construction (e.g., Ihara & Feldman 2004; Laland et al. 2001), in which changes made by humans to their environments create new evolutionary pressures. The acknowledgment of group-level traits also has obvious importance for the evolution of institutions. The processes of institutional change and evolution have been subjects of interest for economic and political theorists for some time (Aoki 2007; Greif & Laitin 2004; North 1990; Young 1998) and have more recently begun to be addressed from the perspective of cultural evolution theory (Bowles et al. 2003; Boyd & Richerson 2008; Richerson & Henrich 2012; van den Bergh & Gowdy 2009). In all these cases, however, the significance of group-level traits has been ignored or downplayed. The incorporation of group-level traits into future models of cultural evolution is crucial.

9. Conclusion

Human groups can manifest structural features and behaviors that are more complex, highly coordinated, fluid, and diverse than groups of any other species. Although the information for

group organization can exist in the minds of individuals, group-level traits cannot be expressed by individuals but only through the coordinated organization of group members. Group-level traits represent an important factor in human ecology and cultural evolution and are categorically different from aggregates of individual-level traits. Traits at the level of individuals are the bedrock of human behavior and encompass the phenomenological experience of being human. But organization matters. Emergent group-level traits allow one group to outperform another, and they alter the physical and social environment, providing additional selection pressures and opportunities for new behaviors. The history of modern humans is to a large extent the history of organization. Researchers interested in the evolution of culture, and in the coevolution of culture and genes, must consider the mechanisms by which group-level traits emerge and evolve.

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NOTES

1. In some social insect colonies, the presence of multiple foundresses leads to low degrees of genetic relatedness. Nevertheless, control of differentiation and organization is still genetic in nature.

2. In evolutionary theory, “ultimate” explanations of a trait deal with the adaptive properties that caused natural selection to favor that trait, whereas “proximate” explanations deal with the immediate physiological and developmental mechanisms that give rise to the trait in an

organism. Laland et al. (2011) discuss how feedback between organism and environment complicates this distinction.

3. Both Read (1958) and Ridley (2010) make compelling cases for the complexity and interconnectedness of technologies, but they also conclude that this complexity supports the case for unconstrained free markets, which I do not believe follows necessarily from their premises.

4. The adaptive fitness of group-level traits, as with individual-level traits, is of course dependent on the selective environment. In a densely treed forest, the organizational properties of the Roman Legion may hinder rather than help, leading to domination by less encumbered Barbarians.

5. Explanations for the loss of complex technology in Tasmania have been proposed that do not rely explicitly on group-level traits, but instead rely on success-based biases in social learning (Henrich 2004b; Powell et al. 2009). Nevertheless, the arguments made in this target article imply that group organization and differentiated roles are crucial (and missing) parts of the Tasmanian story.

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