

construction theory, and paleoanthropological data sets creates a key venue to test the theories presented in the article.

For example, there is archaeological evidence for symbol construction, formation, and use that predates the appearance of *Homo sapiens* (circa 200,000 years ago). Initial results from our broad-scale assessment of these data indicate support for Richerson et al.'s assertion that CGS was active "as far back as symbolic marking is evident." While they suggest symbol-making may go back to 164 k.y.a., there are earlier signs such as the engraved bones from Bilzingsleben (Mania & Mania 1988) which may date to 350 k.y.a. Ochre use older than 200 k.y.a has been uncovered at sites in Zambia (Clark & Brown 2001), Sudan (Peer et al. 2004), and the Netherlands (Roebroeks et al. 2012), suggesting complex behavior and possible CGS at earlier dates. We suggest that key aspects of CGS emerged previous to identifiable symbol-making and then coevolved, via niche construction and selection (alongside drift and gene flow), with that capacity to develop a baseline for the radical leaps in complexity in the last 20,000 years that Richerson et al. focus on.

While we are supportive of the CGS concept, there is a lack of explicit connectivity to the Extended Evolutionary Synthesis (EES). Despite introducing three forms of cultural group selection, Richerson and colleagues retain a reliance on selection-based processes as the key architect of function. This misses the opportunity to engage with niche construction, evo-devo, phenotypic plasticity, and other processes in the EES under which "Organisms are constructed in development, not simply 'programmed' to develop by genes. Living things do not evolve to fit into pre-existing environments, but co-construct and co-evolve with their environments, in the process changing the structure of ecosystems" (Laland et al. 2014, p. 162). The processes in the EES, in addition to selection models, and multiple patterns of evolutionarily relevant inheritance (genetic, epigenetic, behavioral, and symbolic; e.g., Jablonka & Lamb 2005) are central to the development of a more robust CGS approach. The current article does invoke non-genetic inheritance and implicitly uses a form of niche construction but does so without serious connection to the theoretical toolkit available. CGS will be more robust if it were explicitly connected to the EES.

We would be remiss if we did not note that cultural F_{ST} does not function in the same way as a genetic F_{ST} does. F_{ST} measures the variation that exists when a metapopulation lives in discrete groups. However, the assumption that responses to one or two questions on a survey are analogous to "one or two loci for a genetic F_{ST} " is not correct. Variance used to calculate F_{ST} in genetic or morphological contexts are based on physically definable measurements, but the answers by Saudi and Lebanese citizens to one of two questions about the role of clergy in the political system are not truly quantitative measures. They are influenced by multiple contextual and contingent (and linguistic) cultural variables and cannot be treated as independent material measures analogous to the number of alleles at a locus or inter-parietal breadth on a cranium. It is not clear that a cultural F_{ST} measures what a genetic one does or that such a measure is actually useful for assessing CGS.

CGS is relevant and should be incorporated into our understanding of human evolution, but approaches and analyses need to be rooted in a contemporary evolutionary theory and the archaeological record, be untangled from certain assumptions about selection and fitness, and seek models and assessments appropriate for cultural processes.

Societal threat as a moderator of cultural group selection

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Abstract: As scholars have rushed to either prove or refute cultural group selection (CGS), the debate lacks sufficient consideration of CGS's potential moderators. We argue that pressures for CGS are particularly strong when groups face ecological and human-made threat. Field, experimental, computational, and genetic evidence are presented to substantiate this claim.

The debate on cultural group selection (CGS) would be more fruitful if it considered the role of human ecology as a critical moderator of CGS. In particular, we argue that ecological and historical threats to human societies strengthen CGS pressures. As we summarize below, there is substantial evidence from field, experimental, computational, and genetic studies suggesting that exposure to threat increases the strength of social norms and punishment of deviance, which are conditions that Richerson et al. identify as important mechanisms that maintain intergroup variation. Hence, ecological and historical threats can critically moderate the strength of CGS pressures and may provide insight into precisely where, when, and to what extent CGS occurs.

Field research across 33 nations first documented the connection between ecological and historical threat and the degree of norm strength in groups (Gelfand et al. 2011). Ecological and human-made threats were theorized to increase the need for clear rules and coordination for the purpose of survival – whether it is to reduce chaos in nations that have high population density, to effectively deal with resource scarcity, to coordinate in the face of natural disasters, to defend against territorial threats, and/or to contain the spread of infectious disease. Societies facing these ecological and human challenges therefore develop strong norms and sanctions for deviance (i.e., are *tight*) to enhance coordination and deal effectively with such threats. By contrast, societies with less threat have a lower need for coordination, and hence are *loose*, that is, have weaker norms and much higher tolerance for deviant behavior. Using archival and survey data, we tested this hypothesis across a wide range of variables and found that societies facing ecological and historical threats do indeed develop stronger norms and punishment of deviance (Gelfand et al. 2011).

Further research confirmed this relationship at the state level in the United States. Harrington and Gelfand (2014) found that tighter states (e.g., those which have strong norms and punishment of deviance) have a greater degree of natural disasters and environmental vulnerabilities, fewer resources (indicated by greater rates of food insecurity), a greater incidence of disease and health vulnerabilities, and perceive a greater degree of external threat, reflected in the desire for more national defense spending and greater rates of military recruitment, as compared to loose states. (i.e., those which have weaker norms and less punishment of deviance). Individuals in tighter states also had higher levels of conscientiousness – a personality dimension that reflects greater impulse control, cautiousness, desire for orderliness, and conformity to norms – and lower openness – a personality dimension that reflects non-traditional values and beliefs, interest and curiosity toward new ideas, and tolerance for other cultures (John et al. 2008). Tighter states also had significantly lower residential mobility and supported more isolationist policies (such as buying American products exclusively and supporting government restriction of imported products) compared to loose states.

Beyond these correlational results, evolutionary game theoretical (EGT) models show that groups that face a high degree of threat *require* stronger norms and greater punishment of deviance in order to survive (Roos et al. 2015). Following existing EGT models (Hilbe & Traulsen 2012; Roos et al. 2014), we examined the evolution of strategies for cooperation as well as strategies for a subsequent punishment phase in cooperation and coordination games. We found that exposing populations to higher degrees of threat – implemented through lower base-rate payoffs – led to an increase in the survival of agents that adhered to the cooperation or coordination norm and those that punished norm-deviating behaviors. Under low threat, the evolutionary pressures resulted in a more diverse mix of all possible strategies. Besides showing that strong norms and punishment of deviance emerges under chronic levels of high threat, these models also found that temporary increases in threat cause norm strength to increase until the threat subsides. Given that conformity and punishment are important pressures for CGS (per Richerson et al.), it follows that increases in ecological and historical threat contribute to the conditions for CGS to occur.

Our electroencephalography work has also found neurobiological differences in the detection of deviant behaviors among tight and loose groups (Mu et al. 2015). Chinese samples, which reported higher degrees of territorial threats, had stronger neurological responses (e.g., greater N400) in the frontal region when viewing social norms violations (e.g., Bob is in the library, he is shouting as compared to Bob is in the library he is studying) in comparison with U.S. samples. Moreover, stronger N400 responses mediated cultural differences in a number of attitudes and behaviors, including higher self-control and ethnocentrism, but lower creativity, among Chinese as compared to U.S. groups. More generally, pronounced neural reactions to norm violations should enable groups to enforce social norms and punish deviant behavior, which, according Richerson et al., should further enhance intra-group cohesion and intergroup variation.

Relatedly, using genetic data, Mrazek et al. (2013) argue that higher frequencies of short (S) allele in the 5-HTTLPR polymorphism of the serotonin transporter gene (SLC6A4) persist in regions of the world prone to ecological threat because heightened threat sensitivity may be adaptive in such regions. Because the S allele has been associated with more aversive reactions to moral violations in groups, they suggest that threat-driven genetic variance in the S allele may underlie differences in moral attitudes across cultures. Their path model linking ecological threat, genetic variability of the S allele, the strength of social norms, and reactions to moral violations provides plausible evidence for this argument.

In sum, as scholars have rushed to either prove or refute cultural group selection, few have explored it as a phenomenon that is modified by the ecological and historical contexts in which human groups are embedded. Considering the role of societal threat in theories of CGS could help resolve the debate of where, to what extent, and how CGS occurs.

A framework for modeling human evolution

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Abstract: Culture-led gene-culture coevolution is a *framework* within which substantive explanations of human evolution must be located. It is not itself an explanation. Explanations depend on such concrete historical evolutionary factors such as the control of fire, collective child-

rearing, lethal weapon technology, altruistic cooperation and punishment, and the mastery of complex collaboration protocols leading to an effective division of social labor.

The target article nicely elaborates the strong relationship between cultural group selection and gene-culture coevolution. Richerson et al. correctly observe that gene-culture coevolution significantly strengthens genetic group selection models in the literature. All such models employ the *phenotypic gambit* (Grafen 1984), in which complex transmission processes are treated as though they were the product of a single allele of the genome. Such models represent equally any transmission process, cultural, genetic, or interaction between the two, that depend only on vertical transmission from parents to offspring (Gintis 2014).

The target article's contention that cultural group selection is "a basic explanation for our species' highly unusual ability to create large societies with widespread cooperation between non-relatives" (sect. 7, para. 2) is incorrect. Cultural group selection is not an explanation of anything. Rather, it is a *framework* within which such an explanation can fruitfully be developed. The main features of human cooperation, which include collective child-rearing without a reproductive division of labor (Hrdy 2000; Wilson 2012), hunting large game with lethal weapons (Wrangham & Carmody 2010), altruistic cooperation and punishment (Bowles & Gintis 2011), as well as collaborative skills depending on a *theory of mind* (Tomasello 2008), follow from the particular evolutionary history of our species.

Curiously, the authors suggest that there is evidence for culture-led gene-culture coevolution only "for a few simple genetic traits" (sect. 2.2, para. 6). In fact, there is overwhelming evidence for this process as central to the constitution of *Homo sapiens*, a few pieces of which I will cite here.

Human Self-domestication: Darwin noticed that selective breeding of mammals for tameness entailed a pattern of similar side-effects of domestication to human society in distinct species. Darwin even suggested that, "Man in many respects may be compared with those animals which have been long domesticated" (Darwin 1871, Ch. 7, p. 172). Belyaev (1979) corroborated this insight, studying captive silver foxes bred for tameness. These animals developed humanly attractive faces with short snouts, floppy ears, patches of white fur on their heads, and curly tails (Gibbons 2014). More recently, Cieri et al. (2014) documented domesticated syndrome changes in human evolution since the Middle Stone Age and Upper Paleolithic, and Wilkins et al. (2014) have proposed a general genetic model explaining the domestication phenomenon.

This is evidence for a very straightforward culture-led group selection mechanism in which an increasingly complex division of labor and social norms that rewarded cooperation (Tomasello 2014) favored genetic changes that produced a more domesticated and prosocial human disposition.

Control of Fire and the Reorganization of the Human Upper Torso: Prior to the control of fire, hominins inhabited trees at night as a defense against predators. Because predators have an instinctive fear of fire, the control of fire permitted hominins, who were already bipedal, to abandon climbing almost completely (Wrangham & Carmody 2010). The lack of need for brachiation freed the hand, arms, and shoulders of proto-humans to evolve for other purposes (Gintis et al. 2015).

Lethal Weapons and the Physiology of Throwing: Hominins developed the use of long-range projectile weaponry, and such techniques were central to human social life (Bingham 1999; Wilkins et al. 2012). Humans are unique in possessing the neural machinery for rapid manual-brachial movements that allows for precision stone-throwing, which depends on the brain's capacity to orchestrate a series of rapidly changing muscle movements (Calvin 1983).